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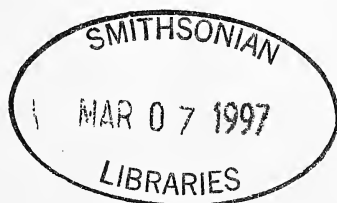
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THE CARNEGIE
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REVISION OF THE WIND RIVER FAUNAS, EARLY EOCENE OF
CENTRAL WYOMING. PART 13. SYSTEMATICS AND PHYLOGENETIC
PATTERN OF EARLY EOCENE *HYOPSODUS*
(MAMMALIA: CONDYLARTHRA)

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ABSTRACT

Hyopsodus is the most common Eocene mammal in western North America, making it an excellent candidate for the study of evolutionary change in a mammalian genus through time. Analysis of numerous dental specimens of Wasatchian and early Bridgerian age indicates that considerable variation existed within what are considered here species of the genus. The nature and pattern of this variation were assessed by evaluation of dental characters and size among specimens that were separated by relative temporal age. This approach led to the identification of two anagenetically evolving "species lineages"—that is, lineages of *Hyopsodus* that demonstrate directional shifts in the frequency and degree of character expression through time. These lineages are *Hyopsodus paulus* (intermediate-sized and spanning most of the Eocene) and the larger *Hyopsodus powellianus* (present from the middle early Eocene through the earliest middle Eocene). Species lineages are divided into successive, informal segments in order to reflect relative age and morphologic differences. Three other small-sized taxa show relationship to *Hyopsodus paulus* at different times during the lineage's history. From oldest through youngest, these species are *Hyopsodus loomisi*, *Hyopsodus minor*, and *Hyopsodus minusculus*. *Hyopsodus loomisi* and *Hyopsodus minor* may also represent a lineage. One other taxon, *Hyopsodus* sp., cf. *H. mentalis*, is present in the early Eocene of New Mexico and, apparently, Wyoming. However, its relationship to other *Hyopsodus* and its geographic distribution remain poorly understood. Naming lineages and branches of lineages or cladistically resolving relationships using conventional systematic approaches is difficult because of the fundamental difference between Recent and fossil species.

INTRODUCTION

Hyopsodus (Figure 1) is one of the most ubiquitous Eocene mammalian genera; collections throughout the United States boast thousands of dental remains, usually isolated teeth and maxilla or mandible fragments. In comparison to dentitions, postcranial material is surprisingly rare. Gazin (1968) gives an excellent comparative survey of *Hyopsodus* postcranial material.

Most *Hyopsodus* were probably no more than 30 cm in length with an elongate body plan—vaguely like the modern ermine (Gazin, 1968). *Hyopsodus* retains the primitive full eutherian complement of teeth, yet the semicrescentic pattern of the molar cusps and lophs is unique. The limbs are relatively short and unspecialized and the anterior incisors somewhat large; suggesting to some a partly arboreal, omnivorous niche (Matthew, 1915a) or, alternatively, a more fossorial habit (Gingerich, 1974a). These questions aside, *Hyopsodus* must have often been a major constituent of North American Eocene faunas.

No derived appendicular or dental characters definitively suggest a relationship between *Hyopsodus* and any of the modern orders of mammals. *Hyopsodus* continues to be consistently referred to the paraphyletic order Condylarthra. Previously it had been considered an ungulate (Cope, 1875; Abel and Cook, 1925), a

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Fig. 1.—Restoration of *Hyopsodus*.

primate (Marsh, 1875; Schlosser, 1887; Matthew, 1899) or close to the Insectivora (Lydekker, 1885; Wortman, 1903; Loomis, 1905).

Matthew (1915*a*, 1915*b*) placed *Hyopsodus* within his emended order Condylarthra (essentially as used today but excluding the Peripitychidae), corroborating Pavlov's (1887) preliminary observations. Simpson (1937) included peripitychids in the Condylarthra and placed many Paleocene genera within the family Hyopsodontidae, a classification maintained in his 1945 monograph on mammalian systematics. Van Valen (1978) has since separated the hyopsodontids from the mioclaeneids, both considered subfamilies of the Hyopsodontidae by Simpson. Hyopsodontid resemblances to artiodactyls (e.g., Simpson, 1937:231) and South American "ungulates" (Paula Couto, 1952) have also been noted. Cifelli's (1982) study on condylarth petrosal structure does not appear to support these or other suggested affinities, at least among the genera examined. Condylarth systematics remain stifled by the lack of skull, anterior dentitions, and postcranial material for many genera. Of the North American Paleocene hyopsodontids, "*Aletodon*" *quadravus* (Gingerich, 1983) (but not *A. gunnelli* of Gingerich, 1977) may be dentally most similar to *Hyopsodus*, more so than *Haplomylus*, which has tradi-

tionally been allied with *Hyopsodus* (Van Valen, 1978). The relationship of *Hyopsodus* to other condylarths remains unclear and will not be understood until a comprehensive review of the condylarths is undertaken.

Hyopsodus first occurs in the latest Paleocene (Clarkforkian Land Mammal Age; see Rose, 1981) and by the early Eocene is either the most common or one of the most common North American mammalian faunal elements. *Hyopsodus* decreases in numerical prominence after Bridgerian time but persists through the Uintan. One species, *Hyopsodus sholemi*, is found at the ?Duchesnean Shoddy Springs locality (see Krishtalka, 1979, for the most recent revision of later Eocene *Hyopsodus*).

Robinson (1966:54) called *Hyopsodus* taxonomy a "systematist's nightmare." *Hyopsodus* material is so abundant and its occurrence in faunas so pervasive that it is difficult to assess the morphologic variability or relationships of species unless stratigraphically detailed analysis is performed. The last comprehensive review of *Hyopsodus* was Gazin's 1968 monograph, a study that considerably simplified the systematics of the genus. However, the taxonomic criteria he used consisted of little more than molar length reckoned with prevailing species nomenclature. Additionally, the stratigraphic resolution of the collections examined was relatively coarse by modern standards. Unfortunately, many of the older collections, although very large, simply lack the precise (or accurate, in some cases) locality data necessary for systematic or evolutionary study. Systematic revision is also hampered because most type specimens lack this information. More recent work with *Hyopsodus*, although stratigraphically sound, has dismissed dental characters (aside from size) and their variation.

As stated by Bown and Rose (1987), "... there has been no published study of dental morphology and dental variability in *Hyopsodus* since Gazin's (1968) work, and very little there." Recent (1975–1990) collections of *Hyopsodus* made by the Carnegie Museum of Natural History, Texas Tech University, and the University of Colorado, Boulder, from the Wind River Basin, Wyoming, and, to a lesser degree, the San Juan (New Mexico) and Bighorn (Wyoming) basins, have much better stratigraphic control. This new material allows a reevaluation of not only the systematics and dental variability of early Eocene *Hyopsodus*, but also of its pattern of evolution. Given the abundance of fossil material, an analysis of *Hyopsodus* should shed new light on these questions and possibly even indicate whether these questions are appropriate.

Abbreviations used in text and tables are as follows: Institutional: ACM—Amherst College Museum, Amherst, Massachusetts; AMNH—American Museum of Natural History, New York, New York; ANSP—Academy of Natural Sciences, Philadelphia, Pennsylvania; CM—Carnegie Museum of Natural History, Pittsburgh, Pennsylvania; UCM—University of Colorado Museum, Boulder, Colorado; UCMP—University of California Museum of Paleontology, Berkeley, California; USNM—United States National Museum, Washington, D.C.; UW—University of Wyoming, Laramie, Wyoming.

PREVIOUS INVESTIGATIONS

Hyopsodus, since its initial description in 1870 (Leidy), has had an interesting and somewhat confusing history of investigation. Problems have included lack of stratigraphic control in many early collections, lost type specimens, and the misconception that the dentition of *Hyopsodus* is so variable in morphology that

distinction of species is impossible (Gazin, 1968:16; Gingerich, 1974a:107; West, 1979a:4). The latter opinion has caused the most recent work on *Hyopsodus* to be primarily statistical in nature.

This study focuses on the systematics and phylogenetic pattern of early Eocene *Hyopsodus* (Wasatchian through earliest Bridgerian Land Mammal Ages). A history of the taxonomy of Wasatchian and early Bridgerian *Hyopsodus* is given in Table 1. A more thorough history of investigation of *Hyopsodus* is provided by Gazin (1968).

The species listed in Table 1 have been subject to various revisions within the last century. A history of revision is given here in an attempt to reintroduce species and remarks on their morphology that have been subsequently ignored or forgotten.

Bridgerian *Hyopsodus* was revised by Matthew (1909) who described its postcranial anatomy for the first time. He synonymized *Hyopsodus vicarius* with *H. paulus*, and described as new the skull of *Hyopsodus despiciens*, which he suggested was the same species as Osborn's (1902) skull of *H. paulus* from the Washakie Basin.

In 1915(b), Matthew recognized Loomis' *Hyopsodus simplex* as characteristic of Sand Coulee beds and the somewhat younger "Gray Bull" horizons of the Bighorn Basin. Characters he considered diagnostic included comparatively small third molars, weak hypocones on M^1 and M^2 , and weaker premolar cingula.

In the same paper, Matthew designated topotypes for both *H. mentalis* and *H. miticulus*, as the holotypes were already missing. *Hyopsodus miticulus* was retained for specimens from the San Juan Basin and material larger than *Hyopsodus simplex* from the Gray Bull. Matthew noticed a somewhat stronger hypocone in *H. miticulus* as well as a more quadrate exterior cone (paracone) on P^4 . Collections of dental remains of this species were already large and Matthew commented on the variability of many tooth characters in *Hyopsodus miticulus*. Matthew also retained Cope's *Hyopsodus mentalis* from the Largo beds of the San Juan Basin and considered *Hyopsodus lemoinianus* to be conspecific with it. Larger size (compared to *H. miticulus*) was cited as chiefly diagnostic of this species, although other characters given by Matthew include a distinct entoconid and hypoconulid on M_3 , large hypocones on M^{1-2} , and a large external cone on P^{1-3} . Lower molars of this species were described as being more elongate. Matthew used *Hyopsodus mentalis* for intermediate-sized individuals (smaller than *H. powellianus*, larger than *H. minor* and *H. minusculus*) from the Lost Cabin zone of the Wind River Basin and from upper beds of the Bighorn Basin. A more detailed tracking of change in variability through time was severely constrained by an inadequate biostratigraphic framework.

Matthew named the new subspecies *Hyopsodus mentalis lysitensis* for specimens from the Wind River Lysite that he regarded as "intermediate in size and progressiveness" between *H. miticulus* and *H. mentalis* (both of the latter species were known to be lithosympatric in the San Juan beds).

Matthew applied *Hyopsodus wortmani* to small *Hyopsodus* from the Wind River Lost Cabin beds; very small Lysite specimens were assigned to the subspecies *H. wortmani minor*. He also commented on the probable relationship of *Hyopsodus mentalis* and *Hyopsodus wortmani* to the Bridger forms *H. paulus* and *H. minusculus*, a logical conclusion that has not been considered in the recent literature (see Gazin, 1968, and West, 1979a). Matthew mentioned the "progressive"

Table 1.—Chronologic summary of the named species of *Hyopsodus* from Wasatchian and early Bridgerian strata. Biostratigraphic age of type is listed.

North America	
1. <i>Hyopsodus paulus</i> —Leidy, 1870. Type species. Type specimen probably Blackforkian in age.	
2. <i>Hyopsodus gracilis</i> —(Marsh, 1871). Transferred to <i>Microsyops</i> (Leidy, 1872) and <i>Notharctus</i> (Cope, 1872). Later made type species of <i>Smilodectes</i> (Wortman, 1903). Specimen Blackforkian in age.	
3. <i>Hyopsodus minusculus</i> —Leidy, 1873. Type specimen Blackforkian in age.	
4. <i>Hyopsodus vicarius</i> —(Cope, 1875). First described as <i>Microsyops vicarius</i> (Cope, 1873). Type specimen Twinbuttean in age.	
5. <i>Hyopsodus miticulus</i> —(Cope, 1877). First described as <i>Esthonyx miticulus</i> (Cope, 1874). Type specimen from San Juan Basin, Wasatchian in age. Specimen lost.	
6. <i>Hyopsodus mentalis</i> —(Cope, 1877). First described as <i>Antiacodon mentalis</i> (Cope, 1875). Type specimen from San Juan Basin, Wasatchian in age. Specimen lost.	
7. <i>Hyopsodus speirianus</i> —(Cope, 1880b). Made the type species of <i>Haplomylus</i> (Matthew, 1915b).	
8. <i>Hyopsodus lemoinianus</i> —(Cope 1882a). Type specimen from Bighorn Basin, probably Lysitean in age.	
9. <i>Hyopsodus powellianus</i> —Cope, 1884. Type specimen from Bighorn Basin, probably Lysitean in age.	
10. <i>Hyopsodus wortmani</i> —(Osborn, 1902). Type specimen from Wind River Basin, probably Lostcabinian in age.	
11. <i>Hyopsodus simplex</i> —(Loomis, 1905). Type specimen bears label "Tatman Mountain." Graybullian or Sandcouleean in age.	
12. <i>Hyopsodus minor</i> —Loomis, 1905. Type specimen from Wind River Basin, Lysitean in age.	
13. <i>Hyopsodus browni</i> , <i>H. lawsoni</i> , <i>H. jacksoni</i> —(Loomis, 1905). Specimens from Wind River Basin, Lysitean in age.	
14. <i>Hyopsodus walcottianus</i> —(Matthew, 1915b). Type specimen from Wind River Formation, probably Lostcabinian in age.	
15. <i>Hyopsodus latidens</i> —(Denison, 1937). Type specimen from Indian Meadows Formation, north-eastern Wind River Basin, Wasatchian in age.	
16. <i>Hyopsodus loomisi</i> —McKenna, 1960. Type specimen from northwestern Colorado Four Mile locality, Sandcouleean in age.	
17. <i>Hyopsodus pauxillus</i> —Gingerish, 1994. Type from Wasatchian 5 interval, Clark's Fork Basin, Graybullian in age.	
Europe and Asia	
1. <i>Hyopsodus jurensis</i> —(Rutimeyer, 1891). Specimens referred to <i>Dichobunidae</i> by Schlosser (1894) and Stehlin (1906). From the Eocene of Switzerland.	
2. <i>Hyopsodus orientalis</i> —Dashzeveg, 1977. From Eocene beds of Mongolia.	
3. <i>Hyopsodus wardi</i> —Hooker, 1979. Type specimen from Eocene Blackheath beds of England.	
4. <i>Hyopsodus itinerans</i> —Godinot, 1981. Type specimen from Eocene Rians region of France.	

nature of the fourth upper and lower premolars of *Hyopsodus wortmani*, but only in comparison with older Gray Bull *H. miticulus*.

Also in this review, Matthew named the species *Hyopsodus walcottianus* from the Wind River Lost Cabin and allied it with the somewhat smaller (but still large) Lysite taxa *Hyopsodus powellianus* and *H. powellianus browni*.

Kelley and Wood (1954) revised the Wind River Lysite record of *Hyopsodus*

as part of a review of the Lysite fauna. Their analysis involved statistically testing four populations defined by morphology. The results indicated the presence of two commonly occurring taxa: *Hyopsodus powellianus* (including *H. jacksoni* and *H. browni*) and *Hyopsodus mentalis*. The holotype and, apparently, the only specimen of *Hyopsodus minor* was retained as a discrete species based on its extremely small size. *Hyopsodus minor* was not considered to be a subspecies of *H. wortmani*, differing from Matthew's (1915b) conclusions. Kelley and Wood held that *Hyopsodus mentalis* specimens were variable, with some resembling the type (probably a topotype) and others approaching *H. wortmani*, although no characters were given.

Kelley and Wood also noted other dental variations in *Hyopsodus*. In *Hyopsodus mentalis*, these included the presence of a P_4 metaconid, prominence of the hypoconid on P_4 , and strength of the lower molar paraconid. In *Hyopsodus powellianus* the P_4 metaconid was said to be variably strong, as was the molar paraconid. M_3 s of *Hyopsodus powellianus* were shown to exhibit highly variable heel development, with the hypoconulid differing in size and its consequent effect on the structure of the molar talonid.

Kelley and Wood (1954) reiterated Matthew's reservations that specimens of *H. powellianus* from the Wind River Basin were smaller than those from the Bighorn Basin, but did not use Matthew's subspecies designations for the Wind River material.

The earliest Wasatchian record of *Hyopsodus*, as reported by McKenna (1960), consisted of two species—*H. miticulus* and a new smaller species that he named *Hyopsodus loomisi*. *Hyopsodus loomisi* included some specimens referred by Loomis (1905) and Denison (1937) to *Hyopsodus simplex* (from the Bighorn Sand Coulee beds and the Indian Meadows Formation, respectively). According to McKenna, the formal diagnosis of *H. simplex* described variability typical of both *H. miticulus* and *H. loomisi*, hence they could not be discriminated based on lower dentitions. Since the stratigraphic provenance of the type of *H. simplex* is incompletely recorded, McKenna hesitated in using it as comparative material for earliest Eocene *Hyopsodus*. *Hyopsodus simplex* was recorded by Loomis as being collected from Sand Coulee beds, but Matthew (1915b) and Denison (1937) state that the type is actually from significantly higher strata, within the Graybull beds. McKenna suggested that lower molar proportions and P_4 paraconid development do not distinguish *H. simplex* from *H. miticulus*. McKenna strengthened the case of dismissing *Hyopsodus simplex* by stating that the type differed from the referred specimens in featuring well-developed entostylids and a multicusped M_3 talonid heel.

As mentioned earlier, Gazin (1968) provided the only recent comprehensive review of the species of *Hyopsodus*. Most of his data relevant to systematic review consists of histograms of the measured length of the lower second molar. The collections available at the time were tied to the known biostratigraphic record. As Cope's San Juan Basin taxonomy had priority, Gazin applied it in constructing a systematic framework for Wasatchian *Hyopsodus*. Significantly, Gazin synonymized *Hyopsodus mentalis* with *Hyopsodus miticulus* and referred to the latter all intermediate-sized *Hyopsodus* species from the entire Wasatchian, including *Hyopsodus simplex* and *Hyopsodus lemoinianus* (from the Bighorn Basin), Matthew's *H. mentalis lysitensis* (Lysite Member of the Wind River Formation), and *Hyopsodus latidens* (Denison, 1937). Gazin assigned small specimens to *Hyopsodus wortmani* except for those from the very earliest Wasatchian. Thus, *H.*

wortmani was seen by him to encompass material from the Wind River, Buffalo, Green River, Bighorn, and Huerfano basins, including the Lysite record of *Hyopsodus minor*. However, the small *Hyopsodus loomisi* from the Sand Coulee beds was retained due to its more primitive molar structure.

For resolving large-sized *Hyopsodus*, Gazin retained some subspecies designations for geographical variants. *Hyopsodus powellianus* was maintained for large specimens from Lysitean strata of the Bighorn Basin, with the smaller subspecies *H. powellianus browni* (Matthew, 1915b) recognized in the Lysite Member of the Wind River Formation. Lost Cabin Member specimens were referred to *Hyopsodus walcottianus*, chiefly on the basis of their larger size.

Gazin's review of early Bridgerian species was more straightforward, and he allocated all intermediate-sized material to *Hyopsodus paulus* (Leidy, 1870). The type of *H. paulus* is probably from Bridger B strata and is extremely numerous in all Blackforkian deposits. *Hyopsodus minusculus* was retained as a small species. Gazin also recognized these species at Powder Wash (Utah). Gazin noted that in the late Bridgerian Twin Buttes horizons these two species do not commonly occur together; only an intermediate lineage is present in early Bridger C (also noted by West, 1979b).

At the time of Gazin's (1968) review, 17 species of Wasatchian and early Bridgerian *Hyopsodus* had been proposed in the literature. He reduced these to seven, with some possible subspecies present in discrete geographic areas. Two European species, probably of early Eocene age, have since been added (Hooker, 1979; Godinot, 1981). Within this more stable taxonomic framework, recent work has begun to document the rate and pattern of *Hyopsodus* evolution.

Gingerich (1974a) employed the early Eocene record of *Hyopsodus* in a stratophenetic analysis supportive of gradual evolution. Although not specifically a revision of the genus, Gingerich dealt with *Hyopsodus* lineages from tightly controlled stratigraphic sequences ranging from the earliest Wasatchian through the earliest Lostcabinian of the Willwood Formation. All of these lineages were defined by graphically plotting \log_{10} of the product of length times width of the first lower molar, a practice defended elsewhere (Gingerich, 1974b). However, Gingerich's graphic portrayal of these data suffers from some conceptual drawbacks. In order to follow this method, the investigator must make *a priori* decisions about the acceptable variation of a category—in this case, size-defined taxa of *Hyopsodus*. As Gingerich's figure (1974a:14, fig. 1) suggests, some of the lineages from different horizons range widely in variation about the mean. In some cases they are arbitrarily split into two clusters representing two taxa; in other cases, this range is lumped into one taxon. Single specimens, that in other horizons could be easily incorporated into a population range, are sometimes isolated as "forerunners" of later emerging taxa. Since the \log_{10} length/width operation must be performed after the data set (in this case, a *Hyopsodus* taxon) has already been defined, it is of little surprise that the resulting pattern is indicative of the original hypothesis.

Gingerich applied taxonomic names to his lineages. These included a *H. loomisi*–*H. miticulus*–*H. lysitensis*–*H. wortmani* lineage (early Graybullian through Lostcabinian), *H. simplex* (derived from *H. loomisi* in the Graybullian), a *H. latidens*–*H. minor* lineage derived from the main stem in late Graybullian times and persisting through the Lysitean, and the large-sized lineage *H. powellianus*–*H. walcottianus* (stemming from *H. lysitensis* in the mid-Lysitean). Mensural data, as cited by Gingerich, does not support an ancestor–descendant relationship between *Hyopsodus*

minor and *Hyopsodus wortmani*. Gingerich speculated on the derivation of "*Hyopsodus mentalis*," the intermediate-sized Lostcabinian species common in the Wind River Basin, from the large-sized "*Hyopsodus powellianus*" lineage. From the Willwood Formation there is very little data to support this hypothesis.

A similar stratophenetic approach was used in the examination of the Bridgerian *Hyopsodus* record (West, 1979a, 1979b), with evidence presented for a small-sized and an intermediate-sized lineage of *Hyopsodus* in Bridger B rocks. According to West, the proper species names are *Hyopsodus minusculus* (small) and *Hyopsodus paulus* (intermediate).

METHODS OF ANALYSIS

Specimens of *Hyopsodus* examined in this study are primarily from the large Carnegie Museum of Natural History Wind River Formation collections, and, to a lesser degree, from the Bighorn, Piceance, and San Juan basins. Some specific localities are discussed in the text. Land mammal ages and subages follow the definitions of Krishtalka et al. (1987).

The *Hyopsodus* material consists of upper and lower jaws and jaw fragments containing a dentition as well as isolated teeth. All specimens of *Hyopsodus* were examined by locality for the purposes of morphological discrimination of phena and quantitative data collection. Each of the CM Wind River Formation localities was subsequently assigned a relative temporal age as accurately as recent lithostratigraphic and biostratigraphic work within the basin makes possible. Specimens from outside the Wind River Basin were also examined comparatively, but in a less controlled stratigraphic context. Table 2 lists localities along with relative stratigraphic, chronologic, or assemblage position. Locality information is on file in the Section of Vertebrate Paleontology, Carnegie Museum of Natural History.

In this study, two complementary techniques were used primarily as methods of analysis. Specimens of *Hyopsodus* from the CM collections were sorted by locality. Data from older collections with less rigorous stratigraphic information were recorded, but were not mixed with data from more recent collections. Maximum occlusal tooth length and width were measured with a calibrated ocular micrometer mounted on a stereoscope. The contribution of cingula and trigonid/talonid shape to these measurements varies but is easily noticeable. Generally, the shape of teeth from any one locality does not differ in its effect on length and width measurements; if it does, it is usually indicative of a derived morphologic condition. Isolated teeth were sometimes measured if tooth position could be accurately assessed, especially in specimens from localities where jaw fragments are rare, such as the earliest Wasatchian Four Mile area. When possible, measurements of isolated molar teeth, with the exception of those from Four Mile, are not included in the histograms presented in this study because of the difficulty of discerning first and second lower molars. The above-mentioned histograms are of the length of the lower second molar plotted against number of individuals. This essentially duplicates the methods of Gazin (1968), and is appropriate for the following reasons: (1) most specimens preserve the lower second molar; (2) the isolated nature of most Wind River Basin exposures and the lack of precise stratigraphic information for the older CM collections from other basins make the adoption of a completely "stratophenetic" approach impractical. Even within the Wind River Formation, lateral sedimentological variation makes precise correlation difficult, especially at the basin margins (Soister, 1968; Stucky, 1984a); (3) the length of the second lower molar is the least variable simple measurement possible (Gazin, 1968; contra Gingerich, 1974b) and is determined relatively rapidly on numerous specimens; (4) direct comparison can be made to Gazin's large database; (5) data can be plotted easily without placing a specimen into a preconceived taxonomic group as Gingerich's (1974a) methods require. West (1979b) presented results from graphing \log_{10} of length times width of the first lower molar against stratigraphic position, as well as length of M_2 against number of individuals from more coarsely defined intervals (e.g., Bridger B of USNM). In both cases, it is possible to determine the presence of two taxa.

A major objective of this study was to investigate dental morphology and its variation in species lineages (defined below) of *Hyopsodus*. Size is not the only determinant for recognizing taxa, contrary to much of the literature (Gazin, 1968; Gingerich, 1974a; West, 1979a, 1979b) concerning species of *Hyopsodus*. Therefore, specimens were examined for derived characters and character frequencies that could be used to discern taxa independently of size. Koch (1986) attributes change in tooth size (but not morphology) in the modern record to cline translocation due to the effects of temperature. Koch also investigated the Eocene record of *Hyopsodus* (using Gingerich's data) in an attempt to find similar patterns within the fossil record. Change in size through time was found to be greater than expected for a clinal translocation model. It seems that this investigation was hindered by an imperfect knowledge of the zoogeographic (as opposed to geologic) distribution of fossil taxa and of paleotemperature

variability. Also, to the best of my knowledge, evolutionary pattern through time has not been demonstrated to have a direct relationship to geographic pattern at any specific time (see also Bown et al., 1994). This may be partly because biologic and paleontologic species are not comparable as they are not defined by the same criteria.

In this study, size is considered one part of the entire character complex that defines the individual. Specimens were assigned (and in many cases reassigned) to taxa primarily on morphologic grounds other than size. The validity of dental characters was then tested against size distribution. In many cases, there was agreement between allocations based on size and all other dental morphology. Using this agreement as an indicator of a valid taxon, it was possible to trace dental morphologies through relative time and subsequently discriminate taxa whose tooth sizes overlap considerably. Conversely, the legitimacy of character and character frequency statements were tested in the face of well-established size trends. After the emergence of some fairly consistent derived characters within lineages of *Hyopsodus*, it became more feasible to note the extent of variability expected within a taxonomic unit. An attempt is made to describe this variability and its overlap. From these data it was possible to construct an internally consistent classification of early Eocene Wind River Formation *Hyopsodus* and compare and refer specimens of *Hyopsodus* from other partly contemporaneous Western Interior basins to this classification. Until there is a consensus concerning the fossil species concept, an internally consistent classification may be one of the most attainable goals of a systematic review.

It was necessary to compare specimens from a wide variety of localities that differ in their stratigraphic or temporal control. For example, because most Gardnerbuttean specimens are from a single locality (Sullivan Ranch, CM loc. 34), it might be argued that these specimens would be expected to show less variability in size and morphology. Therefore, to facilitate comparison, data from the more numerous Lostcabinian localities are grouped together as well as analyzed separately in order to make more valid comparisons.

SYSTEMATICS OF EARLY EOCENE *HYOPSODUS*

In order to establish a useable classification, one applicable to all North American early Eocene localities, it was necessary to adopt a consistent philosophical stance. The systematic conclusions of this study are best understood with knowledge of this position, which is presented here. Preliminary results on the evolutionary pattern of *Hyopsodus* were summarized by Redline (1990a).

The use of a simplified stratigraphic analysis was adopted for two primary reasons. The statistical analyses of Gazin (1968), Gingerich (1974a, 1974b, 1976a, 1976b), and West (1979a, 1979b) suggest that size differences of molar teeth are indicative of some discrete taxa of *Hyopsodus*. Secondly, the morphological variation in upper and lower dentitions is of sufficient magnitude to warrant investigation of material from immediately younger and older strata in order to determine the pattern of evolutionary change and relationship. Detailed analyses of other early Eocene mammals (e.g., *Diacodexis*—Krishtalka and Stucky, 1985; omomyids—Bown and Rose, 1987) have begun to document the nature of evolutionary pattern and rate in other mammalian genera during this time period. Unfortunately, much of this information has been obscured by the search for a suitable nomenclatural solution to apply to the patterns that are apparent. While dental characters are more important than size distribution in diagnosing lineages of *Hyopsodus*, raw size data make an excellent framework for testing hypotheses of relationship. Because this study places a premium on large sample sizes from stratigraphically controlled localities, specimens from areas without adequate biostratigraphic detail were not treated in depth.

Preliminary work with *Hyopsodus* was complicated by difficulty in making taxonomic decisions about material from large collections without information regarding relative stratigraphic position. When specimens were treated in lithosympatric groups, it was discovered that many morphologic character states were normally distributed within clusters, whereas other characters were far more stable (either present or absent). When time (as indicated by biostratigraphy) is superimposed

Table 2.—*Listing of primary study localities.*

Wasatch Formation, northwestern Colorado.

Four Mile loc. CM 953.

Willwood Formation, Bighorn Basin, Wyoming.

J. L. Kay's Graybull localities. CM 140–157.

Hackberry Hollow. CM 878.

Dorsey Creek loc.

San Jose Formation, San Juan Basin, New Mexico.

Almagre. CM 941, 945, 1017–1019, 1021, 1907.

Largo. CM 1025–1027, 1030–1031, 1033.

Debeque Formation, Piceance Basin, Colorado.

Scenery Gulch loc.

Shooty Gulch loc.

Wind River Formation, Wind River Basin, Wyoming.

Cole 1 and 2. CM 1903, 1904.

Lysite Flats 1. CM 928.

Lysite Flats 1A. NW of CM 928.

Lysite Flats 2. CM 793.

Lysite Flats 3. CM 929.

Lysite Flats 3A. CM 930.

Lysite Flats 3B. CM 794.

Lysite Flats 4. CM 931.

Lysite Flats 5. CM 111.

Lysite Flats 6. CM 112.

Lysite Flats 7. CM 802.

Lysite Flats 8. CM 803.

Lysite Flats 9. CM 805.

Lysite Flats 10. CM 800.

Lysite Flats 11. CM 806.

Lysite Flats 13. CM 877.

Lysite Flats 14. CM 801.

Davis Draw A. CM 118.

Davis Draw B and C. CM 797.

Cedar Ridge 1. CM 964.

Cedar Ridge 2. CM 965.

Cedar Ridge 3. CM 966.

Fross Lysite 1. CM 927.

Fross Lysite 1A. CM 1007.

Fross Lysite 5 and 6. CM 1008–1009.

Lysite Rim localities. CM 807, 809–813, 1064, 1091.

Guthrie locality 6. CM 114.

Lysite Flats (nonspecific). CM 130.

Wind River Formation, Wind River Basin, Wyoming.

Okie Trail 1. CM 936.

Okie Trail 2. CM 1049.

Okie Trail 3. CM 1050.

Okie Trail 4. CM 1051.

Okie Trail 5. CM 858.

Viverravus Jaw loc. CM 1550.

Pavillion loc. CM 1952.

Table 2.—Continued.

Wind River Formation, Wind River Basin, Wyoming.

Moneta Hills 1. CM 1046.
 Moneta Hills 2. CM 1047.
 Moneta Hills 3. CM 1048.
 Moneta Hills 4. CM 1541.
 Moneta Hills 5N. CM 1534.
 K-5. CM 1039.
 K-5N. CM 856.
 K-6 (two levels). CM 1040.
 K-7, K-7E, and K-7W. CM 91, 1041, 1042.
 K-8. CM 857.
 K-9. CM 1043.
 K-13 and K-14. CM 1076–1077.
 Lost Cabin near Dubois. CM 99.
 Rate Draw 1. CM 1959.
 Muddy Creek. CM 1910.
 Bridger Creek 1. CM 1542.
 Wild Horse Butte. CM 1011.
 Kay's Lost Cabin SE of Riverton loc.
 Kay's Lost Cabin. CM 88.
 Day Butte. CM 1908.
 Guthrie Lost Cabin 4. CM 90.
 Deadman Butte. CM 1551 (= UCM 80062).
 Red Creek. UCM 79039.
 UCM 80088.
 UCM 79043.

Wind River Formation, Wind River Basin, Wyoming.

Sullivan Ranch (Guthrie loc. 1). CM 34 (two levels).
 K-2. CM 1036.
 K-4 (Train Butte loc.). CM 1038.
 K-15E, K-15W. CM 1078, 1080.
Palaeosyops Jaw loc. CM 1548 (= UCM 81010).
 Someday loc. CM 1545 (= UCM 79040).
 Lightning Butte. CM 1543 (= UCM 80061).
 Rainbow Butte. UCM 80065.
 Sally's Catfish loc. UCM 80064.
 UCM 81026.

onto these distributions, the resulting pattern shows discrete lineages of taxa that demonstrate shifts in frequencies and degrees of expression of morphologic characters through time. Anagenesis is strongly suggested as a cause of this pattern because much morphologic change seems to have occurred without an increase in total taxonomic diversity. This pattern of evolution is very similar to that observed in the early Eocene artiodactyl *Diacodexis* (Krishtalka and Stucky, 1985). The authors of that study used a unique nomenclatural scheme when revising *Diacodexis*, one that describes the phylogenetic pattern of *Hyopsodus* as well.

Hyphenated trinomials (species lineages of Krishtalka and Stucky, 1985) are employed as the most reasonable solution to early Eocene *Hyopsodus* systematics. Only species designations are formally applied, while the third part of the trinomial represents the achievement of an anagenetic grade of character expression by a majority of specimens from a biostratigraphic "population" (a central tendency). The third name of the trinomial is referred to as a segment. Since the nature of lineage transitions through time is often gradational, species-lineage

segments are necessarily delineated arbitrarily. This problem is inherent; work with an extremely dense fossil record of *Hyopsodus* indicates the presence of morphological variation and overlap both between contemporaneous lineages and among lineage segments of the same species that differ in biostratigraphic age. Integrating time and taxonomy in this manner suggests that true biological species have little reality when divorced from the conditions of synchronicity. Given the lack of any knowledge concerning the population genetics of fossil taxa, species-lineage systematics also avoids the problematic and debatable implications of subspecies. Subspecies are firmly rooted in neontology and zoogeography, disciplines dealing with synchronous phenomena.

Lineages furthermore provide a useful conceptual framework for visualizing the iterative evolution of derived taxa from consistently variable stem taxa that persist through time. Lineage segments are no less rigorously delineated than fossil species and have the same utility for drawing biostratigraphic and evolutionary conclusions. While lineage segments do not equal biological species, they represent the lowest-level taxonomic unit observable within *Hyopsodus* outside of the circumstances of absolute penecontemporaneous association. The pattern of *Hyopsodus* dental evolution is real. This pattern has been given the utmost consideration when compared to cladistic methodology and species relationship statements that either: (1) obscure this pattern by ignoring intermediates and variation, or (2) force more precise statements from this pattern than the data afford. The presence of a dense fossil record incorporating relative time is too valuable to ignore and the evolutionary pattern and relationships of *Hyopsodus* could not have been determined without the ability to track change through time.

Successive lineage segments are closely related to one another in an evolutionary sense, but would not always appear so on a cladogram. If a certain lineage segment gives rise to a derived form independently from another earlier or later lineage segment of the same species then, cladistically, the lineage as a whole is paraphyletic. While cladograms can suggest degree of relationship among discrete taxa, they do not describe patterns of evolution well within recognized lineage segments. With increasing documentation of anagenetic change, cladograms have less utility in describing phylogenetic pattern.

The theoretical decoupling of within-taxa anagenesis and speciation is crucial to understanding the phylogenetic pattern of *Hyopsodus*. Evolution, and therefore phylogeny, is a function of time, whereas cladistic analysis documents similarities and differences without regard to time. Neither stasis/punctuation nor gradual evolution can be accounted for in a cladogram. Both demand the analysis of temporal series.

Workers who have discovered similar evolutionary modes in fossil taxa have not agreed on systematic resolution (compare Krishtalka and Stucky [1985] to Bown and Rose [1987] to Martin [1995]). The systematics of *Hyopsodus* proposed here are meant to allow an easily changeable classification in that it makes as few species-level assertions as possible. Perhaps there is a need for consistent taxonomy and approach for instances of dense stratigraphic representation of taxa through time. A cladogram will shed no light on within-species change because its operational units must be discrete, negating the attempt to define continua.

The role of geographic variation is also problematic and should be considered. Geographic variants of *Hyopsodus* are not given taxonomic names in this study; certain key character frequencies seem to ally some of these variants. In the future, the taxonomic method used might also be applied geographically (not as true subspecies unless the evidence can be shown to meet all the biologic requisites) as well

as temporally. Cenozoic temporal resolution, relative abundance of fossil taxa, and fossil species criteria are not now standardized to the point where this is possible.

Following the practice of Krishtalka and Stucky (1985), each lineage segment is represented by a diagnostic series rather than a single type specimen. Holotypes designated in the literature are indicated in both the referred specimens and the diagnostic series sections. A diagnostic series better represents the range of variation observed within lineage segments than a single type and avoids holotypic designations that obviously cannot reflect this variation.

The diagnoses have more meaning when considered as integrated character complexes; in most cases no one character state is diagnostic of all specimens in a lineage. Referred specimens are listed under lineage segments, when appropriate. In instances in which the material preserves no diagnostic features enabling confident classification, the referral is tentative and marked with a "?." Tentatively referred specimens show no morphology that conflicts with the systematic diagnosis of the taxon in question. In instances in which isolated teeth and jaw fragments of more than one species were erroneously catalogued under one CM number, these numbers are referenced in this study as containing discrete taxa "in part." To avoid any confusion, they are not assigned to the diagnostic series of any of the *Hyopsodus* lineages reported here.

Species and lineage-segment diagnoses are relatively long and, in the case of long-lived species, only partly comparative in syntax. This was chosen as the most accurate method of fully describing the nature of character expression and frequency of characters. One reason for doing this is that some dental evolution in *Hyopsodus* is of a mosaic type (see Barnosky, 1993). For example, while the length of P_4 is generally static and then decreases through time in the species *Hyopsodus paulus*, the relative length of the talonid appears to increase until a certain time (Lysitean) and then decreases in proportion to the overall shortening of the tooth. Since species change, but maintain their integrity, a diagnosis cannot fully describe the entire morphologic complex through time. The diagnoses, to a large extent, are entirely new and do not indicate the comparison of new material to a holotype or a diagnosis made on a limited number of specimens. Rather, they are based on comparison of the variability of one temporally constrained "population" to another. The illustrations show both salient diagnostic characters and variability. All were drawn from the same view under upper left side lighting. The specimens illustrated highlight the range of variability typical of the lineage segments.

Lineage-segment boundaries reported here correspond very closely to biostratigraphic boundaries. This is somewhat misleading. Although the terrestrial North American Eocene record is good, it is permeated by gaps that are reflected biologically as well as geologically. This does not mean that morphologic or systematic change occurs only at biostratigraphic or lithologic boundaries; segments are as easily broken into biostratigraphic boundaries as using unfamiliar boundary points.

Statistical and graphic meristic data appear in individually cited tables and figures; a listing of all measured specimens by locality is available in electronic format from the author. A key to frequently used dental terminology is given in Figure 2. The dentition of *Hyopsodus* is exceedingly well known and need not be further described here. A description of the general morphology of all upper and lower teeth is included in Gazin (1968). Type specimens important for comparison are illustrated in Figure 3.

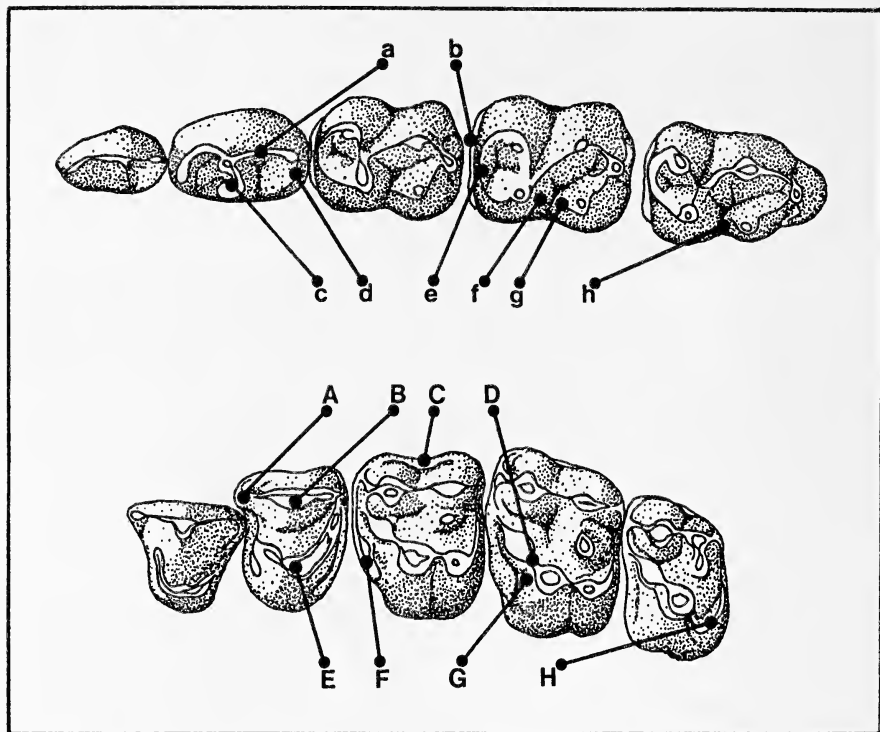


Fig. 2.—Key to *Hyopsodus* dental terminology. Unless designated, term refers to all teeth of a particular series. a, P₄ hypocristid; b, anterior cingulum; c, P₄ metaconid; d, position of P₄ metaconid; e, paralophid; f, position of molar metastylid; g, position of molar entostylid; h, taloid notch, molars and premolars; A, premolar parastyle; B, premolar paracone; C, ectocingula, labial cingula; D, molar protoloph; E, premolar protocone; F, anterior cingulum; G, anterior wall of trigon; H, hypocrista, position of hypocone.

SYSTEMATIC PALEONTOLOGY
 Order Condylarthra Cope, 1881
 Family Hyopsodontidae Lydekker, 1889
Hyopsodus Leidy, 1870

Stenacodon Marsh, 1872.

Lemuravus Marsh, 1875.

Type Species.—*Hyopsodus paulus* (Leidy, 1870).

Known Distribution.—Earliest to late middle Eocene of North America, Eocene of Europe and Asia.

Wasatchian and Early Bridgerian Species.—*Hyopsodus paulus*, *H. minusculus*, *H. minor*, *H. loomisi*, *H. powellianus*, *H. sp.*, cf. *H. mentalis*.

Hyopsodus paulus Leidy, 1870

Microsyops vicarius Cope, 1873.

Hyopsodus vicarius Cope, 1875.

Esthonyx miticulus Cope, 1874.

Hyopsodus miticulus Cope, 1877.

Lemuravus distans Marsh, 1875.

Hyopsodus wortmani (type only) Osborn, 1902.

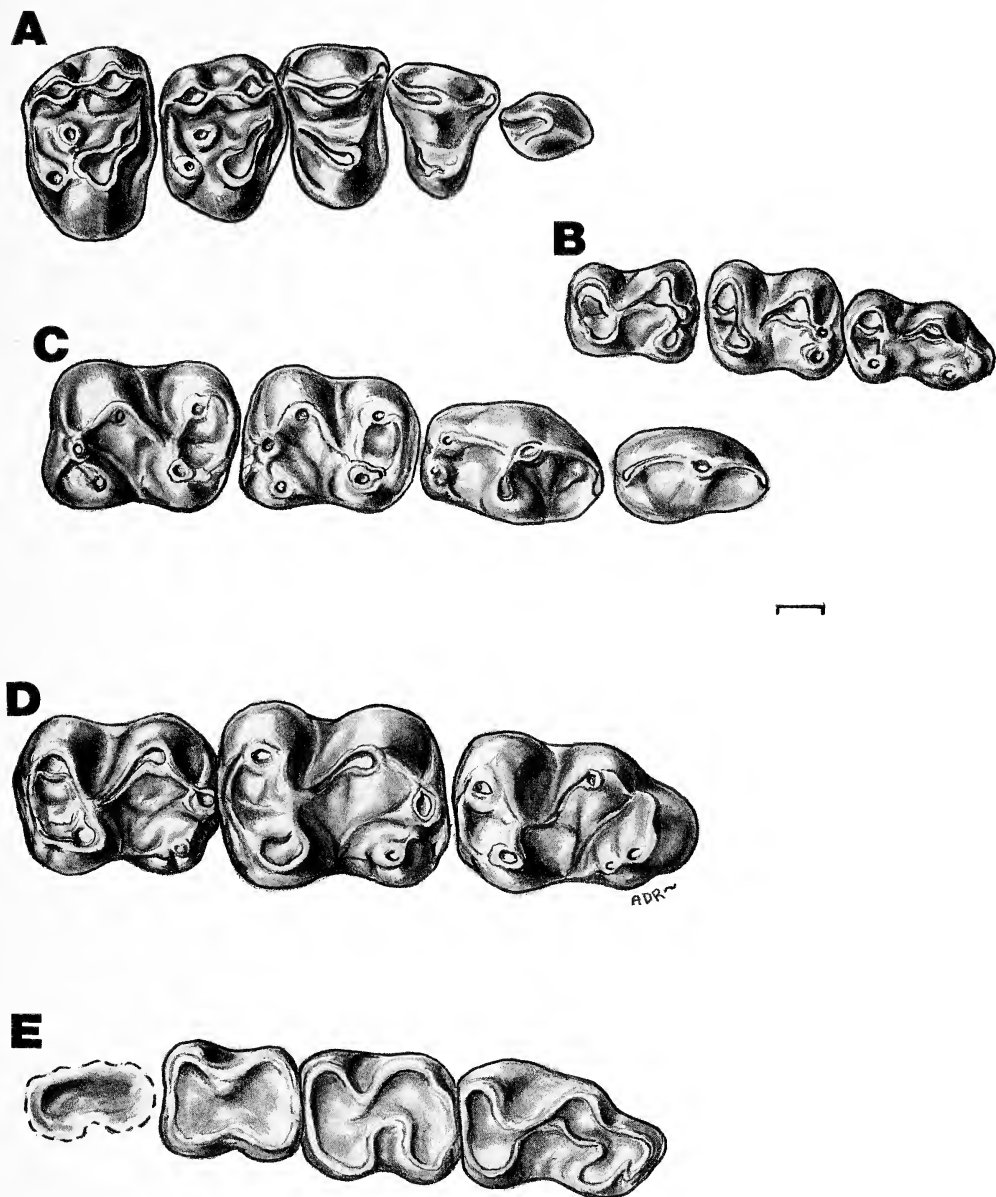


Fig. 3.—Type specimens of *Hyopsodus*. A, UCMP 44781, holotype of *Hyopsodus loomisi*; B, ACM 3492, holotype of *Hyopsodus minor*; C, AMNH 4139, holotype of *Hyopsodus lemoinianus*; D, AMNH 4147, holotype of *Hyopsodus powellianus*; E, USNM 1176, holotype of *Hyopsodus paulus*, type species of *Hyopsodus*. Scale equals 1 mm.

Hyopsodus marshi Osborn, 1902.

Hyopsodus simplex Loomis, 1905.

Hyopsodus despiciens Matthew, 1909.

Hyopsodus mentalis lysitensis Matthew, 1915b.

Hyopsodus latidens Denison, 1937.

Holotype.—USNM 1176, RP₄–M₃. Collected from Smith's Fork of Green River near Fort Bridger, Bridger Formation, Bridger Basin, Wyoming.

Included Lineage Segments.—*Hyopsodus paulus-paulus*, *H. paulus-wortmani*, *H. paulus-lysitensis*, *H. paulus-simplex*.

Diagnosis.—Length of second lower molar between 3.7 and 4.8 mm. Always smaller than *H. powellianus*, smaller than penecontemporaneous *Hyopsodus* sp., cf. *H. mentalis*, larger than *H. minusculus*, *H. minor*, slightly larger than *H. loomisi*. Differing from *H. powellianus*, P³ transverse (labial–lingual) width greater than anterior–posterior length. Differing from *H. powellianus* and *H. loomisi*, parastyle on P³ and P⁴ smaller, but more distinct than *H. minor*. M³ occlusal outline more nearly square than other *Hyopsodus* due to a well-developed, somewhat posteriorly situated metacone. M³ hypocone comparatively better developed than *H. loomisi*, featuring larger basal area where the cusp is confluent with the hypocrista. Upper molar paraconules more robust at base (somewhat crescentic in later lineage segments) where they join the protoloph that runs anterolabially to the junction of the paracone base and anterior cingulum. Anterior cingula and ectocingula of upper molars broader and more deeply excavated than penecontemporaneous lineages of similar or smaller size. Unlike *H. minor* or *H. powellianus*, P₄ talonid with variably developed entoconid. Differing from *H. loomisi*, width of the talonid greater than width of the trigonid on M_{1–2}. Paralophid (anterior cristid of trigonid) inflected slightly anterolingually (more than *H. loomisi*, *H. minor*; less than *H. powellianus*) before ascending to meet the metaconid.

Referred Specimens.—Listed under individual lineage segments.

Known Distribution.—Earliest Wasatchian through middle Bridgerian (Sandcouleean through Blacksforkian) of western North America.

Discussion.—Some of the above-listed characters are shared with larger-sized lineages of *Hyopsodus* and *Hyopsodus minusculus* (indicative of relationship at different levels), but are developed to differing degrees and are associated as parts of discrete character complexes. Temporally adjacent lineage segments of *Hyopsodus paulus* show considerable overlap in frequency and degree of character expression, but because the canalized traits of lineages result in observable morphoclines, the earliest lineage segments do not overlap with the youngest lineage segments. For example, *Hyopsodus paulus-paulus* is quite distinct from *Hyopsodus paulus-simplex*, whereas *Hyopsodus paulus-lysitensis* includes specimens that are not as distinct from the latter. Given the apparent evolutionary rate and mode in *Hyopsodus* (substantiated by change in size of M₁ by Gingerich, 1974a), this phenomenon accurately reflects the true phylogenetic relationships of taxa with an extremely dense fossil record (see Krishtalka and Stucky, 1985: 479).

In this report, the taxon *Hyopsodus paulus* encompasses most specimens assigned to *Hyopsodus miticulus* (as conceived by Gazin, 1968), some specimens of *Hyopsodus mentalis* (Cope, 1875), the holotype of *Hyopsodus simplex* (Loomis, 1905), and *Hyopsodus latidens* (Denison, 1937). In the Wind River Basin, *H. paulus* includes Lysite and Lost Cabin Member individuals referred to *H. miticulus* by Guthrie (1967, 1971), as well as Stucky's (1982) *H. paulus* from the uppermost Lost Cabin Member. The latter specimens show no derived characters that distinguish them from the type or referred Bridgerian specimens of *H. paulus* and are only slightly more primitive than Blacksforkian *Hyopsodus paulus* in

degree of character development.

The species *Hyopsodus paulus* here also includes the type of *Hyopsodus wortmani* (Osborn, 1902). *Hyopsodus wortmani* has long been accepted as a valid species of small *Hyopsodus* from the Wind River Basin, but examination of the holotype (AMNH 4716) has shown that it falls within the range of morphologic and size variability of the Lostcabinian lineage of *Hyopsodus paulus*. Characters of the type specimen supporting this conclusion include the presence of an entoconid on P_4 , a transversely wide M_2 , and the structure of the hypocone on M^3 . The locality information and preservation of this specimen suggest that it was probably collected from the type area of the Lost Cabin Member, which is a Lostcabinian locality. This taxonomic decision is discussed in more detail below. Many other specimens of "*H. wortmani*" collected from the American Museum's Davis Ranch locality (= CM loc. 34) are referred here to *Hyopsodus minusculus*.

Anagenetic character acquisitions in *Hyopsodus paulus*, from Sandcouleean through middle Bridgerian, include: (1) increase in size of upper and lower third molars, increasingly well-developed hypocone on M^3 , more distinct entoconid and hypoconulid on M_3 (also noted by Matthew, 1915*b*); (2) more widely spaced bases of hypocone and protocone on M^1 and M^2 ; (3) labiolingual compression of P^4 paracone; (4) increasingly distinct upper premolar and molar external cingula, particularly the ectocingula; (5) better developed and more distinct external ribs on the upper molar paracone and metacone and the P^3 and P^4 paracones; (6) decreasing robusticity of cusps and increasing lophodonty of upper and lower premolars and molars; (7) increasing height of lower premolar hypocristid and talonid notching of lower premolars and molars; (8) anterior shifting of molar protoconid and hypoconid, lingual shifting of hypoconulid; (9) decreasing anteroposterior length of P_3 and P_4 relative to lower molar length.

Hyopsodus paulus is the most common species of *Hyopsodus* in the Wind River Basin, and also appears to be extremely well represented in the Wasatchian of the Bighorn and Green River basins (following the analyses of Gazin, 1968, and Gingerich, 1974*a*). Among the localities examined here, its presence is indicated (histograms cited under lineage segments) by specimens clustering about a mean lower second molar length of approximately 4.2 mm during the Graybullian through Lostcabinian, and 4.5 mm in the Gardnerbuttean (Table 3). By Blackforkian time, *H. paulus* was the most common species of *Hyopsodus* (West, 1979*a*) and is the most abundant faunal element at most localities (Gazin, 1968). It co-occurs with *Hyopsodus loomisi* at Sandcouleean through ?mid-Graybullian localities, *Hyopsodus minor* in the late Graybullian through Lysitean (possibly earliest Lostcabinian), lineage segments of *Hyopsodus powellianus* in the Lysitean through Gardnerbuttean, and *Hyopsodus minusculus* in the earliest through middle Bridgerian.

The principles of classification utilized in this study imply, artificially by some workers' standards, that *Hyopsodus paulus* was a very long-lived "species" that was present in the earliest Wasatchian. It seems to possess more advanced characters when compared to the lithosympatric *Hyopsodus loomisi* at the Sandcouleean Four Mile locality (McKenna, 1960). Gingerich (1974*a*) gives evidence for only one small *Hyopsodus* form in the basal Willwood; however, both McKenna (1960) and Bown (1979) document two *Hyopsodus* phenae at least this early. The earliest record of *Hyopsodus*, from the Clarkforkian (Rose, 1981), is still very poor. Thus, it cannot be confidently stated whether *Hyopsodus paulus* or *H. loomisi* more closely approximates the primitive condition for *Hyopsodus*,

Table 3.—Summary of statistics, lower dentitions of *Hyopsodus paulus* (lineage segments *H. paulus-paulus*, *H. paulus-wortmani*, *H. paulus-lysitensis*, *H. paulus-simplex*). High, low, mean, SD in mm.

	P ₃ (L, W)	P ₄ (L, W)	M ₁ (L, W)	M ₂ (L, W)	M ₃ (L, W)
<i>H. paulus-paulus</i>					
High	3.4, 2.3	4.0, 2.9	4.6, 4.0	4.8, 4.3	5.5, 3.8
Low	3.0, 2.0	3.3, 2.3	3.9, 3.1	4.2, 3.5	4.5, 3.1
n	10	46	76	114	88
Mean	3.1, 2.2	3.6, 2.6	4.3, 3.6	4.5, 3.9	5.0, 3.5
SD	0.12, 0.09	0.15, 0.14	0.17, 0.17	0.15, 0.18	0.21, 0.14
CV	3.9, 4.1	4.2, 5.4	4.0, 4.7	3.3, 4.6	4.2, 4.0
<i>H. paulus-wortmani</i>					
High	3.4, 2.4	3.9, 2.9	4.3, 3.6	4.6, 3.8	5.1, 3.5
Low	2.6, 1.9	3.0, 2.2	3.6, 2.8	3.8, 3.2	4.1, 2.8
n	17	48	76	88	66
Mean	3.0, 2.1	3.5, 2.5	3.9, 3.1	4.2, 3.5	4.6, 3.1
SD	0.19, 0.14	0.15, 0.14	0.16, 0.16	0.20, 0.13	0.22, 0.14
CV	6.3, 6.6	4.3, 5.6	4.1, 5.2	4.8, 3.7	4.8, 4.5
<i>H. paulus-lysitensis</i>					
High	3.5, 2.5	3.9, 3.0	4.5, 3.8	4.6, 4.0	4.9, 3.7
Low	3.0, 1.8	3.3, 2.4	3.6, 2.9	3.8, 3.2	3.9, 2.7
n	14	51	105	161	124
Mean	3.2, 2.2	3.5, 2.6	3.9, 3.2	4.2, 3.5	4.5, 3.1
SD	0.18, 0.18	0.14, 0.14	0.16, 0.16	0.15, 0.15	0.18, 0.17
CV	5.6, 8.2	4.0, 5.4	4.1, 5.0	3.6, 4.3	4.0, 5.5
<i>H. paulus-simplex</i>					
High	3.3, 2.4	3.7, 2.8	4.1, 3.5	4.4, 3.9	5.0, 3.5
Low	3.0, 2.0	3.2, 2.3	3.4, 2.6	3.6, 3.2	3.7, 2.7
n	11	35	47	79	60
Mean	3.1, 2.1	3.5, 2.6	3.7, 3.1	4.1, 3.6	4.2, 3.1
SD	0.12, 0.13	0.11, 0.10	0.14, 0.17	0.16, 0.14	0.22, 0.13
CV	3.9, 6.2	3.1, 3.8	3.8, 5.5	3.9, 3.9	5.2, 4.2

or which of these species occurs first in the North American fossil record.

Lineage Segment *Hyopsodus paulus-paulus*
(Fig. 4, 5; Tables 3, 4)

Diagnosis.—Largest (mean length of M₂) lineage segment of *Hyopsodus paulus*. Taller, more gracile cusps than pre-Bridgerian *H. paulus*; also generally more lophodont molars. M² paraconule more robust and crescentic in occlusal view than in *H. minusculus*. M³ more rectangular with more distinct hypocone than in *H. minusculus*. Most distinct parastyle within *Hyopsodus paulus*. In contrast to earlier lineage segments, lower molar trigonid more elevated; paraconid almost universally absent. In contrast to *H. powellianus-walcottianus*, molar entostylids infrequent and not inflated. Entoconid and hypoconulid more lingually shifted than other Wasatchian or early Bridgerian *Hyopsodus*, consequent arcuate hypoconid with long posthypocristid.

Diagnostic Series.—USNM 1176 (type, *Hyopsodus paulus*). CM 21089, 21092, 22321, 30932, 35734, 40083, 44957, 44969, 55225. UCM 46599. ANSP 10253, 10256.

Referred Specimens. CM 4953, 21044 (in part), 21046, 21048, 21051, 21054, 21056, 21059–21060,

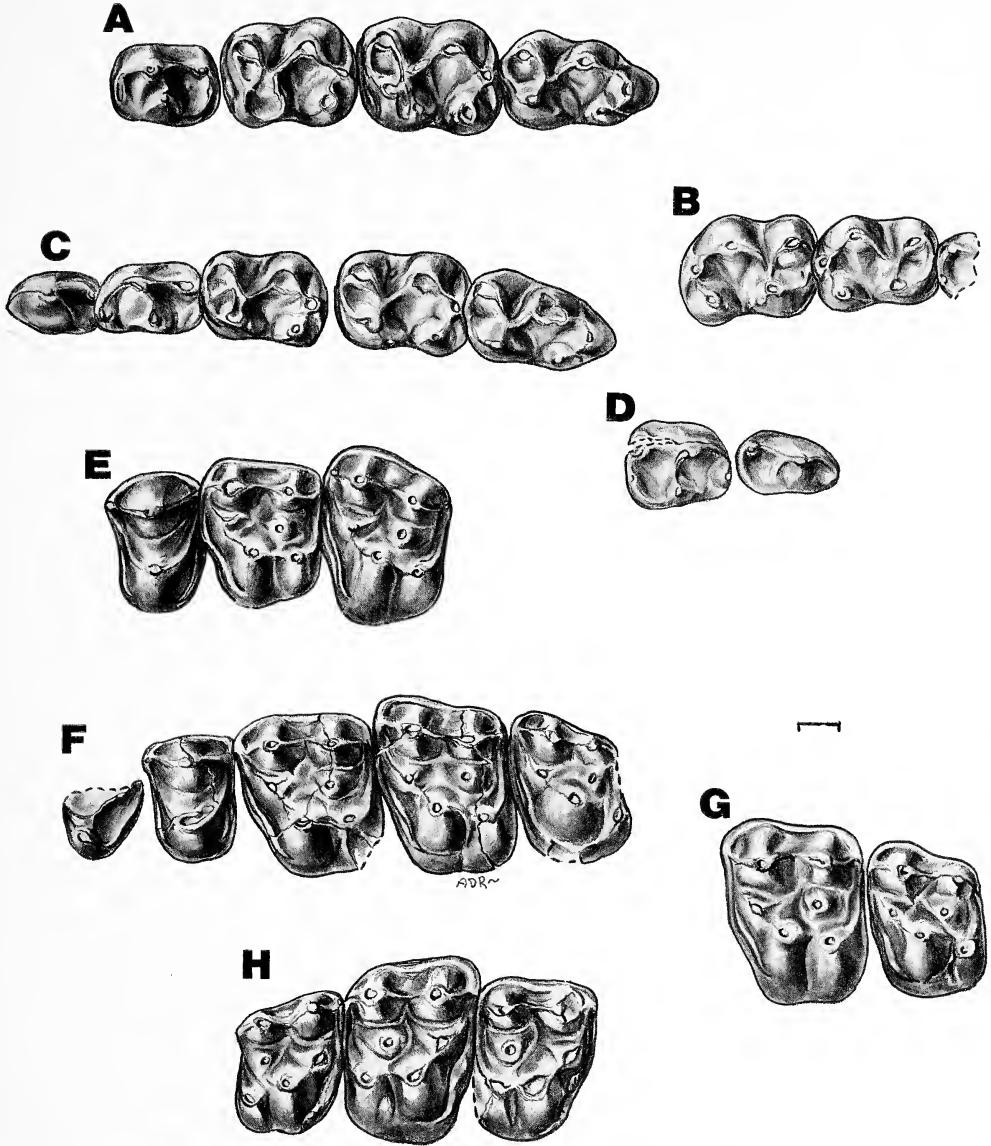


Fig. 4.—Specimens of *Hyopsodus paulus-paulus*. A, CM 36449; B, CM 35722; C, CM 40083; D, CM 36447; E, CM 21092; F, CM 22588; G, CM 55258; H, CM 29126. Scale equals 1 mm.

21062, 21065–21070, 21076, 21078, 21081, 21083–21085, 21088, 21090, 21092, 21095–21096, ?21097, 21101, 21103, 21105, 21107–21108, 21921–21922, 22314–22318, 22320–22323, 22531 (in part), 22588, 27439, 27447–27448, 29125–29126, 29130, 29133, 29135 (in part), 30887–30889, 30895, 30898, 30900, 30903–30904, 30906, 30909, 30916–30917, 30919–30920, 30925–30927, 30930–30932, 30935–30937, 31001, 31004, 31007–31008, 31013–31014, 35721–35731, 35733–35740, ?35741, 35743, 35745, 35747–35752, ?35753, 35754–35757, 35760, 36447 (in part), 36449, 36930, 36941, 36945, 37331 (in part), 37332 (in part), 40081–40083, 40085–40088, 40092, 40094, 40098–40099, 40614–40615, 40617, 40619–40625, 40629–40630, 40633, 40636, 40640, 40645, 40650, 40653, 40655, 40657, 40659, 40661–40662, 40674–40675, 40677, 40752, 44914–44915, 44917–44918, 44923 (in part), 44931–44937, 44940, 44944, 44946, 44955, 44956 (in part), 44957–

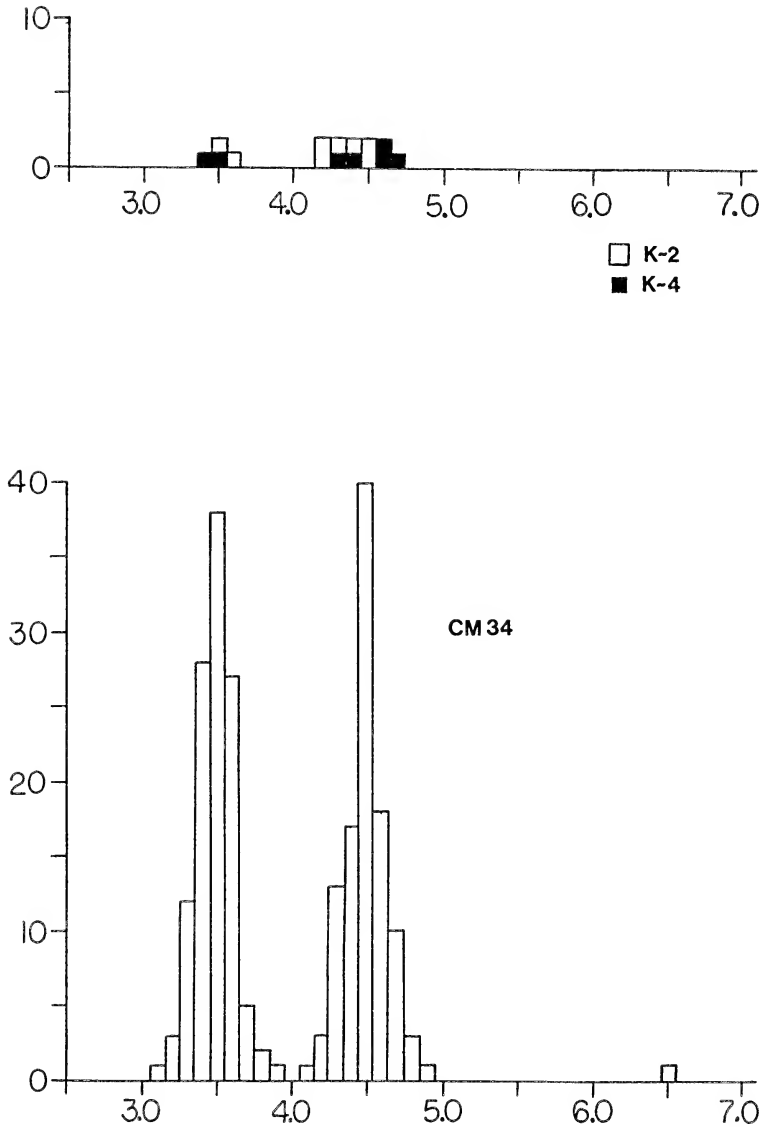


Fig. 5.—Frequency histograms for lower second molars of *Hyopsodus* from Wind River Formation Gardnerbuttean localities. Vertical axis, number of individuals; horizontal axis, molar length in mm.

44958, 44960, 44963–44965, 44967–44970, 44972–44973, 44974 (in part), ?44980, 44981, 44984–44990, 44993–44998, 45163, 45185, 45191–45193, 45284–45285, 45321, 45330, 45959, 45963–45964, 45968–45970, 45972, 45978, 46657, ?47227, 55032, ?55033, 55034, 55036–55038, 55040–55047, 55049, 55051, 55053, 55057, 55059–55060, 55063–55064, 55067–55070, 55072, 55074, 55076–55077, 55079, 55082–55083, 55221–55222, 55225, 55227–55229, 55233–55234, 55238, 55240–55241, 55246, ?55248, 55249–55252, 55255–55256, 55258–55260, 55268–55270, 55272, 55274, 55276–55279, 55283–55285, 55289, 55292–55293, 55295–55297, 55299, 55300–55301, 55304, 55307–55311, 55314, 55316–55317, 55319, 55322, 55324, 55326, 55329. UCM 44831, 44861, 45298, 45300, 45303, 45365–45366, 45430, 46473, 46549, 46586–46589, 46592, 46599. UW 23517, 23527. ANSP 10252–10253, 10255–10256, 10258. USNM 1176 (type, *H. paulus*).

Localities.—CM 34 (Davis Ranch of AMNH), 1036, 1038, 1543, 1545, 1548. UCM 80064, 80065, 81026. UW V89041. ANSP Grizzly Buttes locality (Blacksforkian).

Known Distribution.—Earliest Bridgerian (Gardnerbuttean) of Wind River Basin, Wyoming, and Huerfano Basin, Colorado; Blacksforkian of western North America.

Discussion.—The diagnostic characters described above are best developed in Blacksforkian specimens; Gardnerbuttean specimens are less lophodont overall and somewhat less progressive in the degree of lower premolar shortening and the anterior placement of the molar protoconid and hypoconid. Gardnerbuttean specimens are allocated to *H. paulus-paulus* because they most closely approach Blacksforkian specimens in character acquisition, even though they are often less well developed. As in the Blacksforkian, they are associated with a lithosympatric small *Hyopsodus* lineage. Segment name *paulus* indicates the affinities of Gardnerbuttean specimens to Blacksforkian *Hyopsodus paulus*, but Wind River specimens are overall more primitive in morphology. On the other hand, they are very close to later Bridgerian specimens in size.

In the Wind River Basin, a large sample of *Hyopsodus paulus-paulus* has been recovered from CM loc. 34. At this locality, *H. paulus-paulus* shows a normal distribution of size and character development with virtually no overlap with the smaller, lithosympatric, and penecontemporaneous *H. minusculus*. The smallest specimens of *H. paulus-paulus* and the largest *H. minusculus* approach each other in size (there is no overlap at CM loc. 34) but are distinct in premolar structure and the shape and proportions of the molars.

Hyopsodus paulus appears to be stable in molar size throughout the middle Bridgerian (West, 1979a, 1979b). Although Gardnerbuttean *Hyopsodus paulus* is somewhat more primitive than the type specimen and other Bridger B material examined (e.g., ANSP 10252–10253, 10255–10256, 10258), the majority of specimens possesses all of the diagnostic characters listed above and is similar in size. Dentitions of *H. paulus* from the ANSP Grizzly Buttes locality have taller, more gracile cusps (especially the metaconid), and more lingually shifted and closely placed molar entoconids/hypoconids. The lower premolar series is also shorter. Gazin (1968:16) noted that in Bridgerian *Hyopsodus*, P² is occasionally single rooted, a condition not confirmed in the earliest Bridgerian CM sample.

Hyopsodus paulus-paulus is the final segment of the *Hyopsodus paulus* evolutionary lineage within the Wind River Basin. The work of West (1979a, 1979b) and Krishtalka (1979) indicates that the “species” continues through the Bridgerian into the Uintan. AMNH and ANSP material, as well as CM specimens from the Powder Wash locality of the Green River Basin, show increasing canalization of the traits which first distinguish *H. paulus-paulus* in the earliest Bridgerian. Analysis of later Bridgerian material could well indicate that additional segments of *Hyopsodus paulus* should be recognized and that Gardnerbuttean specimens should relinquish their claim on segment name *paulus*.

Morphologically, *H. paulus-paulus* does overlap with individual specimens of Lostcabinian *Hyopsodus paulus-wortmani*, but *H. paulus-wortmani* is smaller on average, does not uniformly feature a P₄ with a distinct paraconid and a well-developed posthypoconid with an entoconid, and is less lophodont overall. Only a few specimens of *H. paulus-wortmani* are as derived as *Hyopsodus paulus-paulus* in the expression of upper dental characters. Lostcabinian *H. paulus* shares

anagenetic characters with *Hyopsodus paulus-paulus*, but only in comparison to earlier lineage segments of the same species.

At localities where large collections have been made (e.g., CM loc. 34 and CM loc. 1046), *Hyopsodus paulus-paulus* occurs in lithosympatry with *H. minusculus* and the much larger *Hyopsodus powellianus-walcottianus* (Fig. 5), whereas *H. paulus-wortmani* occurs only with *H. powellianus-walcottianus* (see Fig. 7). Importantly, *Hyopsodus paulus-wortmani* shows a normal distribution of dental features later canalized differently by *H. paulus-paulus* and *H. minusculus*. *Hyopsodus paulus-paulus* shares more lophodont molars, especially the hypoconid, shorter P_{3-4} , long M_3 , well-developed ribs on the upper dentition, and stronger molar hypocones and anterior and labial cingula with *Hyopsodus minusculus*. This suggests that both Bridgerian forms are descended from a single Lostcabinian lineage. Robinson's (1966) quantitative data for Huerfano *Hyopsodus* can also be interpreted as indicative of a single, intermediate-sized Lostcabinian species and two discrete (somewhat larger and smaller) Gardnerbuttean lineages.

Robinson (1966), and later, Stucky (1982), applied *Hyopsodus paulus* to Lost Cabin Member specimens in the Wind River Basin; Gazin (1968) and Guthrie (1971) preferred the name *Hyopsodus miticulus* (Cope, 1874, 1877), which was originally based on material from the San Jose Formation. The holotype of *Hyopsodus miticulus* is lost, and the species lacks a diagnosis, making this nomen inappropriate for material from the Wind River Basin.

Gazin's review (1968), based solely on the length of M_2 , indicates that intermediate and small *Hyopsodus* lineages co-occur in the Lostcabinian "Knight Member" equivalents of the Green River and Washakie basins. The stratigraphic resolution of these collections is poorly refined, but if Gazin's conclusions are correct, the co-occurrence of *Hyopsodus paulus-paulus* and *Hyopsodus minusculus* may be typical only of earliest Bridgerian sediments in the Wind River and Huerfano basins. However, earlier work by Gazin (1962) indicated a small form of *Hyopsodus* was common only in the New Fork Tongue, higher stratigraphically than the first occurrence of the "species" *H. walcottianus*. As will be discussed below, "*H. walcottianus*" is most common in Lostcabinian rocks; therefore, New Fork Tongue strata may be younger.

Lineage Segment *Hyopsodus paulus-wortmani*
(Fig. 6-8; Tables 3, 4)

Diagnosis.—Smaller in mean size than *Hyopsodus paulus-paulus*. Intermediate between lineage segments *H. paulus-paulus* and *H. paulus-lysitensis* in degree of lophodonty and gracility of all teeth. Features more frequently and strongly developed than in *H. paulus-lysitensis* include: external cingula on upper premolars and molars; height and compression of premolar paracone and molar paracone and metacone; taller, more gracile molar protocone with less robust base; more distinct ribs on external cusp margins of upper dentition; open molar talonids, entoconid less robust with less frequently developed entostylid; molar trigonid taller with less tendency to exhibit paraconid. Compared to lineage segment *H. paulus-paulus*, *Hyopsodus paulus-wortmani* is less lophodont overall; smaller in mean size; does not uniformly show the diagnostic lower premolar morphology and more rarely exhibits hypoconulid reduction and lingual shifting of posterior talonid cusps on M_{1-2} .

Diagnostic Series.—AMNH 4716 (type, *Hyopsodus wortmani*), 14611. CM

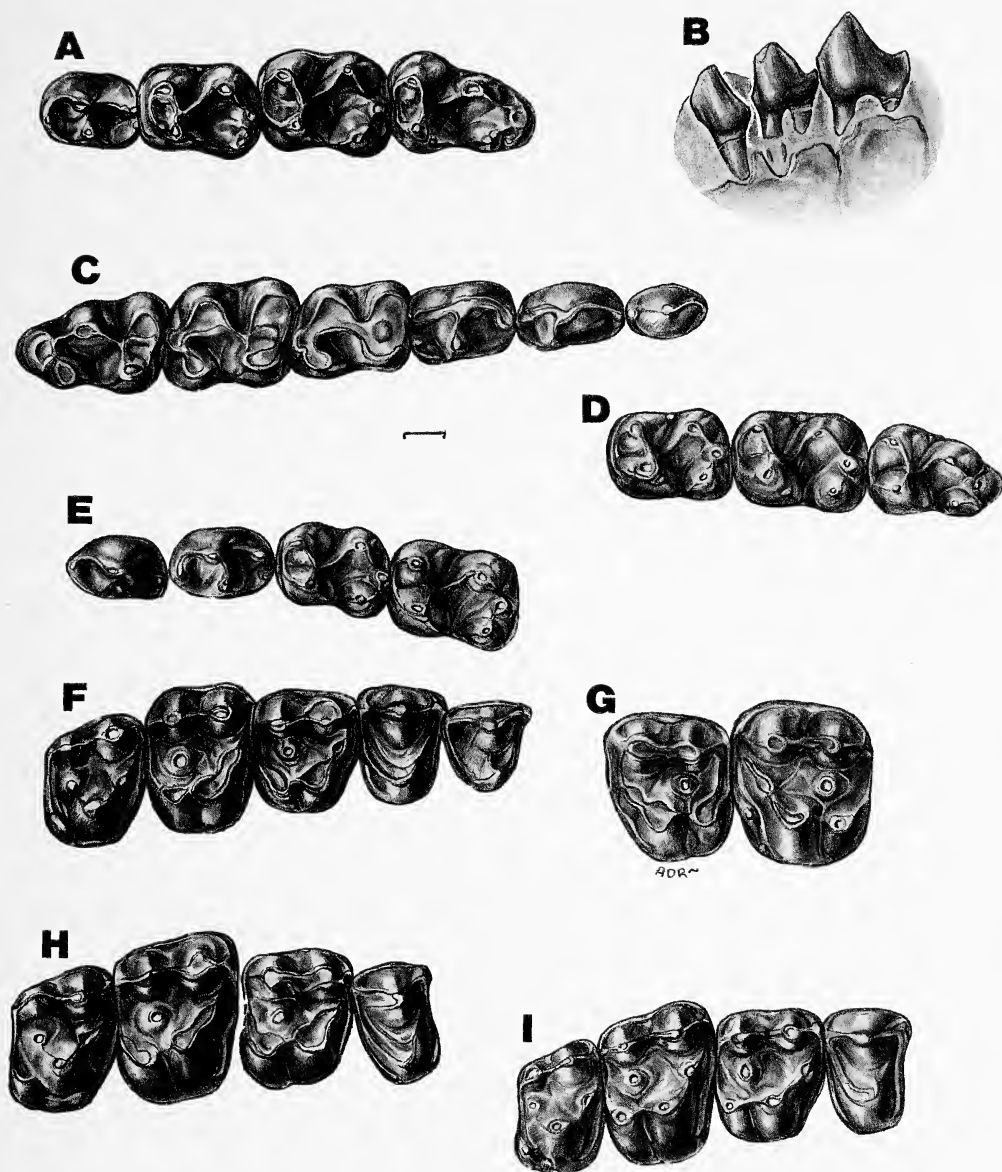


Fig. 6.—Specimens of *Hyopsodus paulus-wortmani*. A, CM 60560; B, CM 60561; C, CM 45233; D, CM 49459; E, CM 45244; F, CM 46647; G, CM 45133; H, CM 45286; I, CM 49458. Scale equals 1 mm.

45152, 45202, 45223, 45244, 45259, 45286, 46647, 47171, 49458, 49460, 60560, 60561.

Referred Specimens.—CM 4959, 21214–21215, 21220 (in part), 22324–22327, 22329–22336, 22338, 22342, 34886, 36452–36455, 37226, 40665–40666, 40669–40672, 40679–40690, 44999, 45151–45152, 45154, 45156–45157, 45200–45231, 45233–45234, 45236–45256, 45258, 45260–45262, 45264–45266, 45268, 45270–45283, 45289, 45291–45295, 45299, 45300–45302, 45304, 45325–45327, 45329, 45932, 45961, 45998, 46644–46645, 46647, 47029, 47040, 47060–47061,

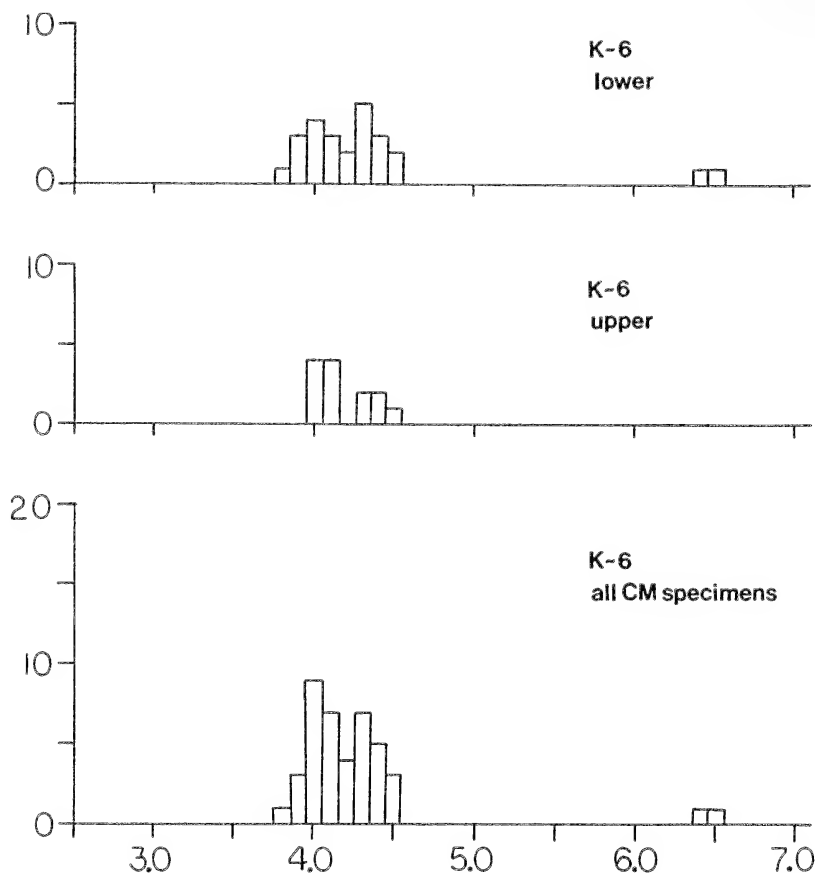


Fig. 7.—Frequency histograms for lower second molars of *Hyopsodus* from Wind River Formation Lostcabinian locality 1040 ("K-6"). Vertical axis, number of individuals; horizontal axis, molar length in mm.

47080–47081, 47102, 47150–47152, 47166–47170, 49440–49444, 49446, 49449–49450, 49452–49457, 49459–49462, 49464–49465, 49477, 60560–60562. UCM 44328–44329, 44332–44333, ?44377, ?44393, 44394, 44414–44415, 44453–44454, 44560–44561, 45334, 45342, 45392, 46352, 46623, 46642–46644, 46797, 46799, 46800–46805, 46935–46937, 46965. AMNH 4716 (type, *H. wortmani*), 14611, 14633. ACM 10091. (Wind River, ?Lysite/?Lost Cabin) CM 34885 (in part), 37333, 40678, 40691, ?45935, 47127, 47129.

Localities.—CM 88, 90–91, 99, 856–857, 936, 1011, 1039, 1040–1043, 1046–1048, 1076–1078, 1080, 1534, 1541–1542, 1550–1551, 1908, 1910, 1952, 1959, Kay's loc. S.E. of Riverton. UCM 79043, 80088. AMNH Buck Springs loc. ACM type Lost Cabin loc.

Known Distribution.—?Late Lysitean and Lostcabinian of Wind River Basin, Wyoming; Lostcabinian of Huerfano Basin, Colorado; late Wasatchian of Bighorn and Green River basins, Wyoming.

Discussion.—The Lostcabinian lineage segment *Hyopsodus paulus*–*wortmani* provides the best documented illustration of the species-lineage evolutionary pattern in early Eocene *Hyopsodus*. This is due, in part, to the good stratigraphic resolution of the Lost Cabin Member in the Wind River Basin. The absolute

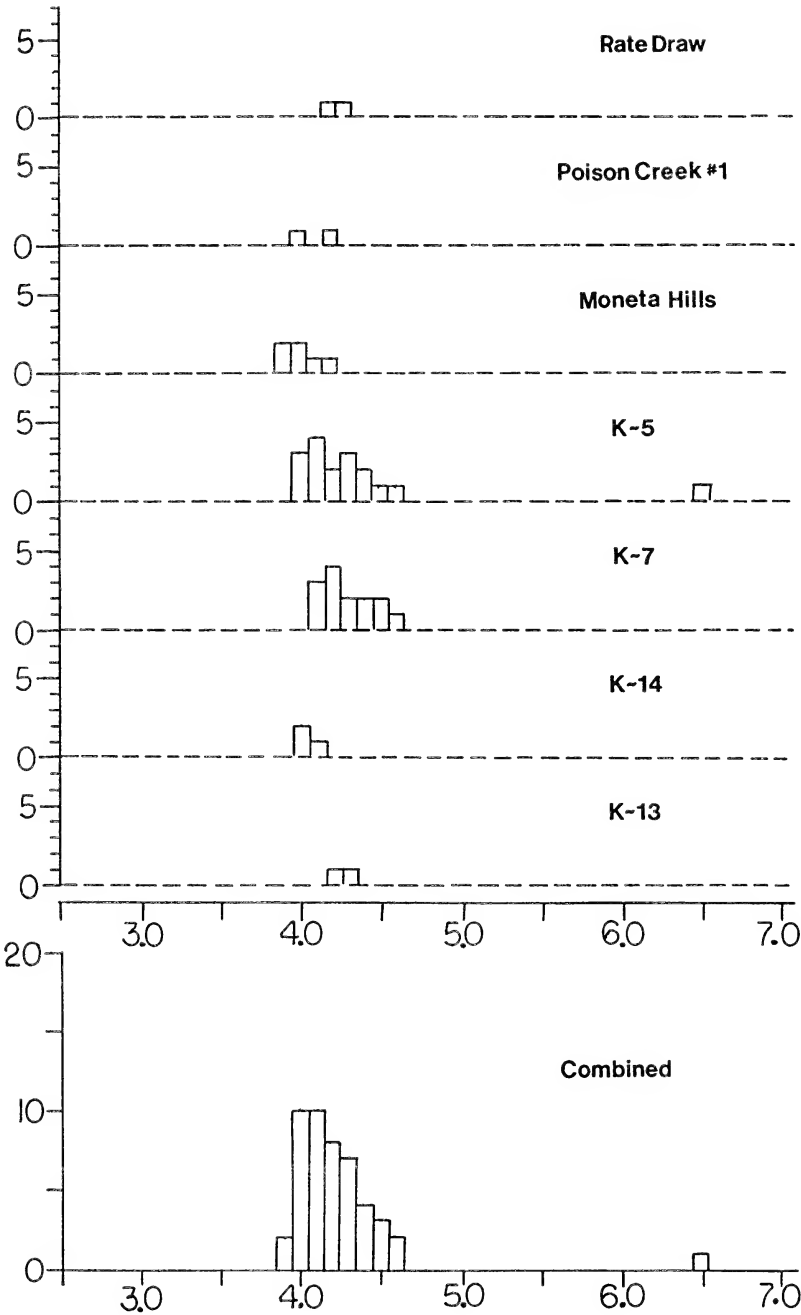


Fig. 8.—Frequency histograms for lower second molars of *Hyopsodus* from Wind River Formation Lostcabinian localities, all data combined on lowermost histogram. Vertical axis, number of individuals; horizontal axis, molar length in mm.

variation in dental morphology is somewhat greater than in Gardnerbuttean *Hyopsodus* (this may be partly explained by the more geographically widespread Lostcabinian localities), but is no greater than Lysitean or Graybullian *H. paulus* or Lysitean *H. powellianus*. An insufficient number of middle Bridgerian *H. paulus* was examined for a confident assessment of character variability; the size of M_1 is quite stable (West, 1979a; 1979b).

In the middle to late Lostcabinian, specific characters that are normally distributed in a single lineage segment (*H. paulus-wortmani*) are later canalized differentially in two coexisting lineages by the early Bridgerian. The consistently varying characters of interest in *H. paulus-wortmani*, also noted to a similar degree in *H. paulus-lysitensis* (see below), are the length of P_3 and P_4 , the development of the hypocristid and entoconid on P_4 , strength and location of P_{3-4} paraconid, architecture of the hypoconulid and entoconid on M_1 and M_2 , degree of expression of M^3 hypocrista, development of the upper molar protoloph and associated paraconule, and the length/width proportions of the upper molars. Histograms of the length of M_2 (Fig. 7, 8) indicate a slightly bimodal size distribution at some Lostcabinian localities, but characters are expressed evenly among the specimens examined. For example, CM 45233, a larger individual, features molar proportions and an open P_4 talonid similar to *H. minusculus* on the one hand, and a P_4 entoconid and overall size closer to *H. paulus-paulus* on the other. CM 45218 is located on the small end of the size frequency distribution (more similar to *H. minusculus*), but M_1 is wide with a well-separated hypoconulid/entoconid as in *H. paulus-paulus*. Significantly, the range of variation is not associated with size, regardless of the taxonomic status of the Lostcabinian sample (two versus one "species") or its resolution. This condition meets the criterion of a single lineage segment in this study.

Hyopsodus paulus-wortmani occurs commonly at middle to late Lostcabinian localities such as CM locs. 1040, 91, and 1046–1047, and also appears to occur at early Lostcabinian CM loc. 1550, the ?early Lostcabinian Okie Trail localities, and CM loc. 1952 (see histograms, Fig. 22). However, too few specimens are, as yet, available from these localities to refer them with certainty to *H. paulus-wortmani* (rather than *H. paulus-lysitensis*). As discussed below, at the Okie Trail and CM loc. 1952, the specimens in question are associated with larger and somewhat atypical *Hyopsodus* not found in the typical Lostcabinian fauna. The "wortmani-morphs" from the Okie Trail are listed with *H. paulus-wortmani* for the present time in order to form a testable hypothesis when more material is discovered. *Hyopsodus paulus-wortmani* is easily distinguished from the much larger and more bunodont *Hyopsodus powellianus-walcottianus* with which it is lithosympatric in the Lostcabinian.

The markedly bimodal size distribution of small and intermediate-sized *Hyopsodus* previously noted in the Lostcabinian of the Wind River Formation (see Lost Cabin frequency histogram in Gazin, 1968) is the result of mixing all collected specimens from the Lost Cabin Member, traditionally thought to represent one Land Mammal Subage. Because a large number of Lost Cabin Member *Hyopsodus* specimens are Gardnerbuttean in age, a Gardnerbuttean size distribution was strongly imprinted on the collective Lost Cabin Member data.

Gazin (1968) noted more elongate, basined fourth lower premolars in specimens of late Wasatchian "Knight Formation" *Hyopsodus*. No such trend is observable in the Lostcabinian of the Wind River Formation, although this character is common in Lysitean *H. paulus*.

There is no morphology in *H. paulus-wortmani* to support Gingerich's (1974a) derivation of Lostcabinian intermediate-sized *Hyopsodus* from the large-sized Lysitean lineage *Hyopsodus powellianus*.

Lostcabinian *Hyopsodus* is referred to *Hyopsodus paulus* rather than *Hyopsodus minusculus* (see below) because its size is slightly closer to early Bridgerian *H. paulus* and because its upper molars are more frequently closer to *Hyopsodus paulus* in the morphology of the protoloph and M³ hypocone. Lower dentitions, both molars and premolars, are with almost equal frequency close in morphology to either *H. paulus-paulus* or *H. minusculus* from the Gardnerbuttean levels of the Lost Cabin Member of the Wind River Formation.

Lineage Segment *Hyopsodus paulus-lysitensis*
(Fig. 9–11; Tables 3, 4)

Diagnosis.—P_{3–4} posthypocristid stronger than in *H. paulus-simplex*; differing from *H. paulus-wortmani*, commonly wraps around talonid and runs anteriorly to the base of the metaconid; P₄ more nearly square than in *H. paulus-wortmani*, P₄ talonid less square than in *H. powellianus*. Compared to *H. paulus-paulus*, lower molars bunodont; entoconid and metaconid lower crowned; molar talonids relatively closed and not deeply notched as in *H. paulus-wortmani* and *H. minusculus*; paraconid more frequently developed on paralophid of M₁. Entostylid common, metastylid variably present and more common than in *H. powellianus*. M₃ hypoconulid lobe often imperfectly separate from entoconid. P⁴ parastyle more anteriorly placed relative to paracone than in later lineage segments. M^{1–3} protoloph not as well developed, less crest-like, and with smaller paraconule than in *H. paulus-wortmani*; hypocone less elevated and somewhat more labially placed on M^{1–2} in majority of specimens.

Diagnostic Series.—AMNH 15621 (type, *Hyopsodus lysitensis*). CM 22703, 39162, 39169, 39172, 39752, 39803, 46841, 49421, 54106. ACM 11078.

Referred Specimens.—(Wind River, Lysite) CM 19811, 19818, 19823, 19825, 19827, 19829–19831, 19836–19837, 19839, 19850, 19851 (in part), 19852 (in part), 19853, 20878–20879, 20920–20925, 20939–20940, 20942, 21789–21790, 21898, 21901–21904, 21907, 21909–21910, 22680, 22687, 22694, 22701–22702, 22710 (in part), 22718 (in part), 22735 (in part), 22736 (in part), 28652–28655, 28657–28663, 28665, 28667 (in part), 28668 (in part), 28669, 28724, 28731, 28733, 28756, 28759, 28760 (in part), 28761 (in part), 28762 (in part), 28764, 28766, 28770, 28774 (in part), 28777, 28778 (in part), 28936 (in part), 28937, 29191–29195, 29196 (in part), 31349–31351, 35891, 35896, 35905, 35909, 35910, 36071, 36072 (in part), 39148, 39158, 39164, 39169, 39171–39172, 39176, 39178, 39181–39183, 39186–39187, 39190, 39192, 39204, 39217, 39231, 39233, 39235, 39237–39238, 39240, 39244–39245, 39279, 39286, 39290–39291, 39293–39295, 39518, 39550, 39569–39570, 39572, 39575 (in part), 39623, 39663, 39668–39671, 39673, 39675, 39685, 39752–39758, 39764, 39777, 39789 (in part), 39792–39794, 39796, 39798 (in part), 39799, 39801, 39803–39805, 39812, 39814–39815, 39819, 39821 (in part), 39822–39823, 39824 (in part), 39825, 39830, 39834, 39835 (in part), 39837–39838, 39840–39841, 39848, 39850, 39852, 39857, 39861 (in part), 39963–39967, 39978–39979, 39980 (in part), 39985, 45305, 45307, 45309–45311, 45313–45315, 45333–45335, 45341, 45344–45345, 45347–45348, 45350, 45353–45354, 45357, 45359–45361, 45363, 45366, 45373, 45375–45376, 45379, 45381–45382, 45383 (in part), 45384, 45388–45391, 45900, 45902–45905, 45906, 45908, 45912, 45914–45915, 45918, 45920–45921, 45923–45925, 45929–45931, 45995 (in part), 45996 (in part), 45997 (in part), 46479, 46482–46483, 46486 (in part), 47008, 47010, 47012–47014, 47261, 47263–47265, 47269–47270, 49404, 49411, 49416, 49421–49422, 49425–49426, 49428, 49431, 49433, 49435–49437, 49439, 49478–49479, 49482–49483, 49486–49487, 49489–49490, 53797, 53803, 53805, 53807–53808, 53811, 53817, 53824, 53830, 53832, 53834, 54094, 54097, 54099, 54101–54102, 54105, 54116, 54119, 54122–54123, 54173, 54176–54178, 54184, 54189–54190, 54193, 54199, 60202. (San Jose Formation) CM 45974–45975, 45977–45978, 45979–45980, 45982, 45986, 45991–45992, 46808, 46817, 46830, 46841–46843, 46887, 46891–46893, 60568–60569, 60576, 60577–60582. ACM 11078. AMNH 4093, 4128, 16199, 86262, 86278,

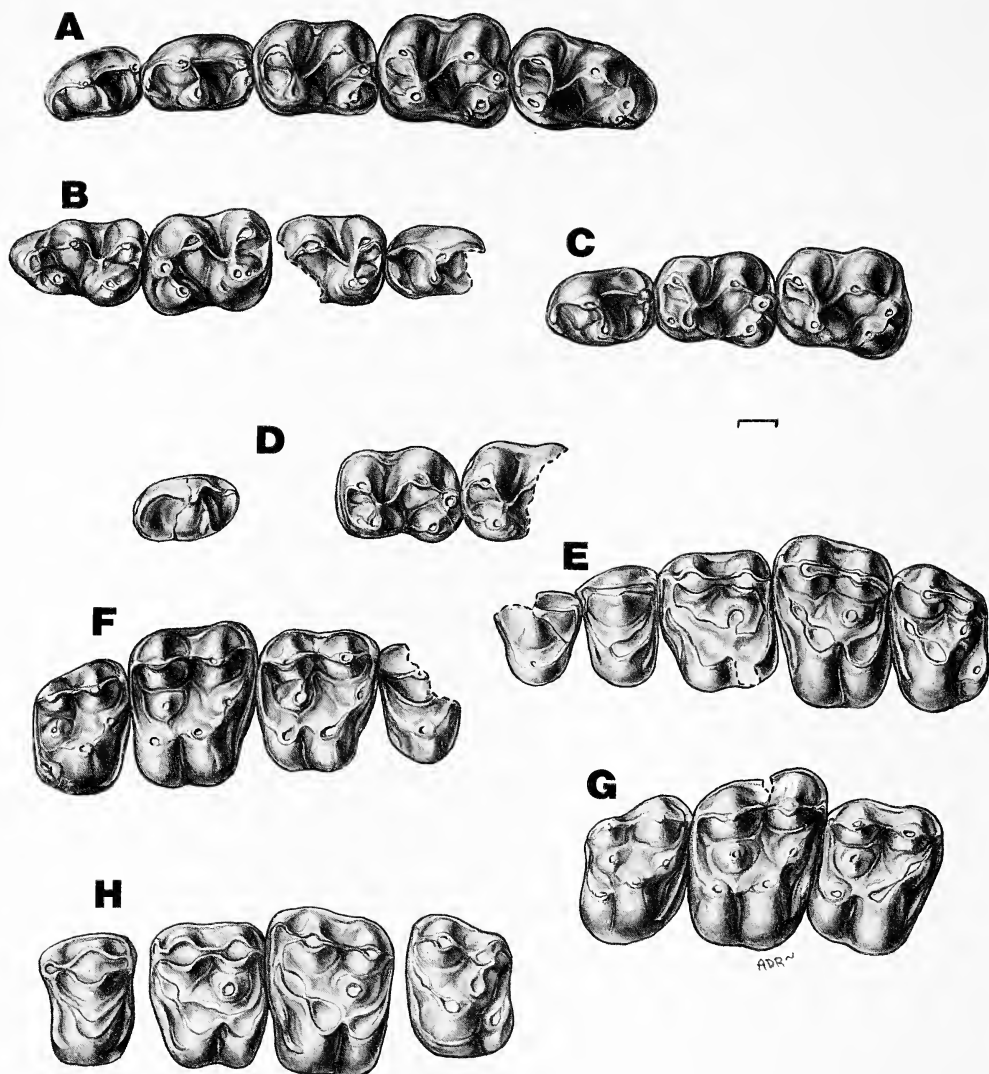


Fig. 9.—Specimens of *Hyopsodus paulus-lysitensis*. A, CM 22703 (lower); B, CM 28662; C, CM 54106; D, CM 19811; E, CM 21909; F, CM 22703 (upper); G, CM 39169; H, CM 39172. Scale equals 1 mm.

93330. (Bighorn Basin, Lysite) AMNH 15621. (Piceance Basin, tentatively referred) CM 4904–4905, 4910, 4916, 4939–4940, 34473.

Localities.—CM 111–112, 114, 118, 130, 793–794, 797, 800, 801–803, 805–807, 809–813, 877, 927–931, 941, 945, 964–966, 1007–1009, 1017–1019, 1021, 1025–1027, 1030–1031, 1033, 1064, 1091, 1903–1904, 1907, Scenery Gulch loc., Shooty Gulch loc. ACM Lysite localities. AMNH 15 Mile Creek loc., Bighorn Basin.

Known Distribution.—Lysitean of Wind River and Bighorn basins, Wyoming; late Graybullian through Lysitean of Piceance Basin, Colorado; ?late Graybullian/?early Lysitean of San Juan Basin, New Mexico.

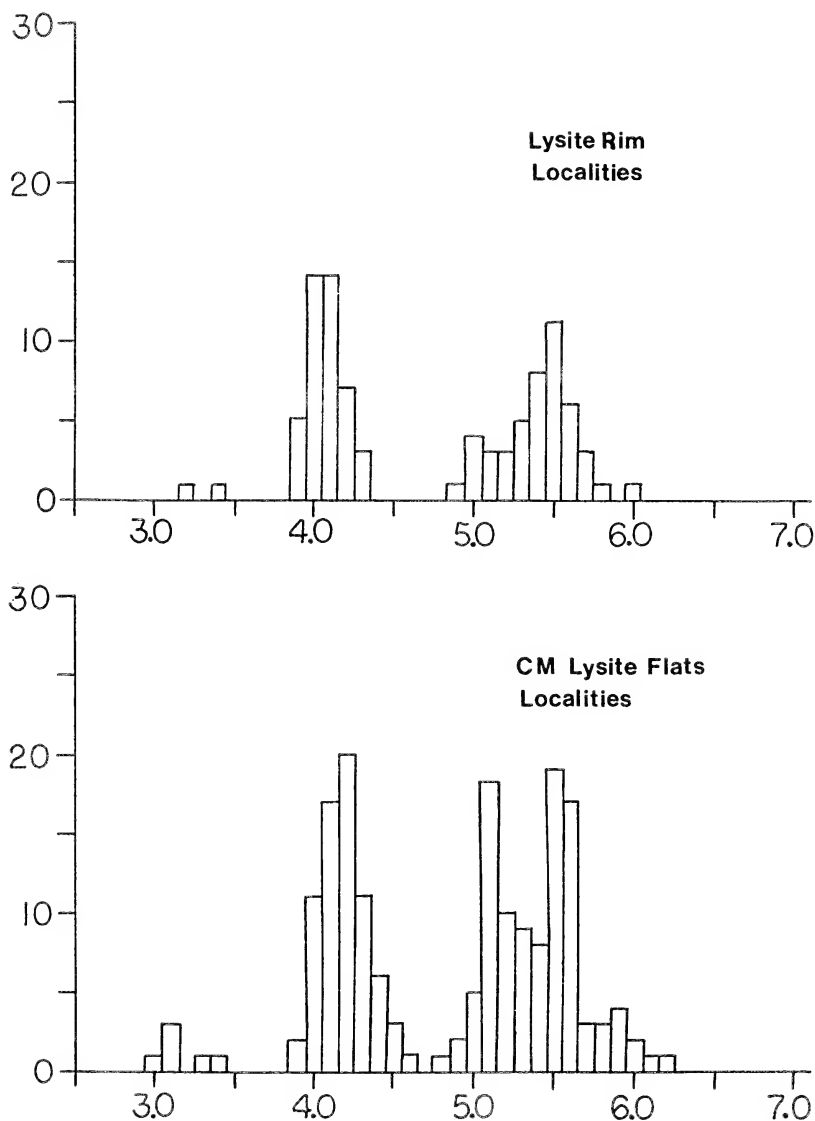


Fig. 10.—Frequency histograms for lower second molars of *Hyopsodus* from Wind River Formation Lysitean localities (second histogram combines all Lysite Flats localities). Vertical axis, number of individuals; horizontal axis, molar length in mm.

Discussion.—*Hyopsodus paulus-lysitensis* is intermediate between *H. paulus-simplex* and *H. paulus-wortmani* in the frequency and development of the following characters: more progressive than *H. paulus-simplex* in size of upper and lower third molars, distinctness of hypoconulid lobe and entoconid on M_3 , lower molar paraconid less frequent in occurrence, upper molars somewhat less bunodont, hypocone more strongly expressed on M^3 , hypocone more closely placed to protocone on M^{1-2} and better developed external cingula on molars and premolars. It differs from *H. paulus-wortmani* as outlined in the diagnosis above, but is very

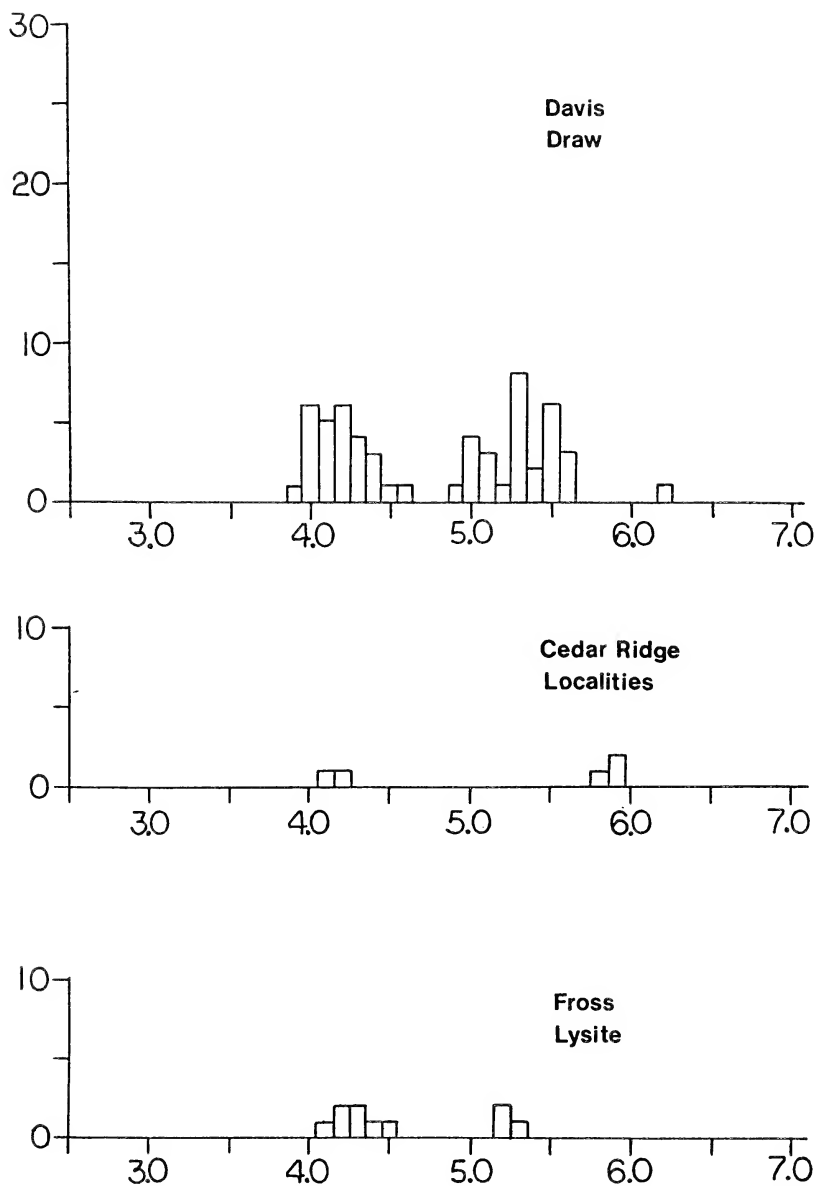


Fig. 11.—Frequency histograms for lower second molars of *Hyopsodus* from other Wind River Formation Lysitean localities. Vertical axis, number of individuals; horizontal axis, molar length in mm.

close to this segment in dental measurements (Tables 3, 4). Aside from relatively minor differences in the frequency of lower premolar morphology and the shorter relative length of M_3 , these segments would be difficult to distinguish.

Guthrie (1967, 1971) referred Lostcabinian *H. paulus-wortmani* and Lysitean *H. paulus-lysitensis* material to the same species, *Hyopsodus miticulus*. The existence of an intermediate-sized lineage of *Hyopsodus* in the Lysite Member of the Wind River Formation has long been acknowledged. Kelley and Wood (1954)

Table 4.—Summary of statistics, upper dentitions of *Hyopsodus paulus* (lineage segments *H. paulus*—*paulus* *H. paulus*—*wortmani*, *H. paulus*—*lysitensis*, *H. paulus*—*simplex*). High, low, mean, SD in mm.

	P ³ (L, W)	P ⁴ (L, W)	M ¹ (L, W)	M ² (L, W)	M ³ (L, W)
<i>H. paulus</i> — <i>paulus</i>					
High	3.5, 3.6	3.3, 4.9	4.7, 5.5	5.1, 6.5	4.3, 5.5
Low	3.1, 3.2	2.9, 4.0	3.7, 4.6	4.1, 5.5	3.6, 4.3
<i>n</i>	4	13	23	37	27
Mean	3.3, 3.4	3.2, 4.4	4.2, 5.0	4.5, 5.9	3.9, 5.0
SD	0.15, 0.14	0.12, 0.23	0.22, 0.26	0.22, 0.26	0.19, 0.29
CV	4.5, 4.1	3.8, 5.2	5.2, 5.2	4.9, 4.4	4.9, 5.8
<i>H. paulus</i> — <i>wortmani</i>					
High	3.4, 3.4	3.1, 4.4	4.4, 5.1	4.8, 6.1	3.6, 4.9
Low	3.0, 3.1	2.7, 3.7	3.5, 4.1	3.6, 4.9	3.0, 4.1
<i>n</i>	5	10	16	21	10
Mean	3.1, 3.2	2.9, 4.1	3.8, 4.6	4.1, 5.5	3.4, 4.6
SD	0.17, 0.10	0.11, 0.20	0.27, 0.31	0.29, 0.35	0.19, 0.21
CV	5.5, 3.1	3.8, 4.9	7.1, 6.7	7.1, 6.4	5.6, 4.6
<i>H. paulus</i> — <i>lysitensis</i>					
High	3.5, 3.6	3.5, 4.6	4.6, 5.6	4.7, 6.1	4.1, 5.6
Low	2.5, 3.1	2.9, 3.9	3.5, 4.3	3.6, 4.9	3.1, 4.2
<i>n</i>	6	19	22	36	25
Mean	3.2, 3.3	3.2, 4.2	3.9, 4.8	4.1, 5.5	3.4, 4.6
SD	0.34, 0.16	0.17, 0.20	0.29, 0.32	0.27, 0.32	0.22, 0.32
CV	10.6, 4.8	5.3, 4.8	7.4, 6.7	6.6, 5.8	6.5, 7.0
<i>H. paulus</i> — <i>simplex</i>					
High	3.1, 3.1	3.3, 4.5	3.9, 5.1	4.3, 5.9	3.5, 4.5
Low	— —	2.9, 4.0	3.4, 4.3	3.6, 5.0	2.6, 3.8
<i>n</i>	1	12	14	22	20
Mean	— —	3.0, 4.2	3.6, 4.6	3.9, 5.5	2.9, 4.1
SD	— —	0.12, 0.19	0.13, 0.19	0.17, 0.21	0.21, 0.22
CV	— —	4.0, 4.5	3.6, 4.1	4.4, 3.8	7.2, 5.4

assigned specimens of this lineage to *H. mentalis*, while Guthrie (1967) believed that the size of Lysite Member specimens agrees better with *H. miticulus*. Analysis of CM and AMNH New Mexican material suggests that Almagre and Largo “*Hyopsodus miticulus*” and some specimens of “*H. mentalis*” are similar to Wind River Lysite material, but show a slightly different distribution of character states and size distribution. Since the holotypes of both these species are lost, these names are probably best not applied to Lysite Member material. The subspecies *H. mentalis lysitensis* (type, AMNH 15621) from Lysite beds of the Bighorn Basin was designated as a Lysite form of intermediate-sized *Hyopsodus* by Matthew (1915*b*). The lineage-segment etymology chosen here reflects his observations. The morphology of the holotype is that most typical of Lysitean *H. paulus*.

In the Lysitean of the Wind River (refer to histograms in Fig. 10, 11) and Bighorn basins, *Hyopsodus paulus*—*lysitensis* coexists in lithosympatry with both the smaller *Hyopsodus minor* and the significantly larger *Hyopsodus powellianus*—*powellianus*. In the Piceance and San Juan basins (Fig. 21), it again is found in association with *H. minor* and a form generally larger than *H. paulus*—*lysitensis*, but smaller than *H. powellianus*—*powellianus*. *Hyopsodus paulus*—*lysitensis* from these more southern basins is referred to *H. paulus*—*lysitensis* separately above, by geographic area. This was done because of their slightly more bunodont, in-

flated molar cusps and somewhat less open molar talonids (much closer to *H. paulus-lysitensis* than to *H. paulus-simplex*) in the majority of specimens. In the San Juan Basin, lower dentitions from the Almagre level are distinct from Largo specimens in the primitively shorter length of M_3 . Some of these differences may be attributable to anagenesis or possibly regional variation.

Variation within *H. paulus-lysitensis* from the Lysite Member of the Wind River Formation includes some individuals that partially overlap both immediately older and younger lineage segments of *H. paulus*. For example, CM 54106 primitively features a well-developed paraconid on M_1 and a shorter, more rounded P_4 with less well-developed hypocrista and hypoconid. On the other hand, CM 22703 and CM 39472 are more gracile, have a longer M_3 and more open, notched talonids on M_{1-3} . Similar variation was noticed in Lysite *Hyopsodus* from the Amherst collections by Kelley and Wood (1954).

Hyopsodus paulus-lysitensis shares with penecontemporaneous *H. powellianus-powellianus* a well-basined, very rarely notched P_4 with frequently strong posthypocristid, larger third molars, variably distinct P_4 metaconid, and strong upper molar protoloph. It differs in the more frequent occurrence of molar metastylids, less anteriorly placed molar protoconid, more commonly distinct pre-molar paraconid, less expanded anterior cingula on M^{1-3} , M^3 hypocone and hypocrista structure, and significantly smaller size. *Hyopsodus minor* is considerably smaller than *Hyopsodus paulus-lysitensis* and has more poorly differentiated, conical cusps and less molariform premolars. In the San Juan and Piceance basins, referred specimens of *H. paulus-lysitensis* differ from *H. sp.*, cf. *H. mentalis* primarily in their smaller size and in lacking wide P_4 talonids and frequently large entoconids.

Lineage Segment *Hyopsodus paulus-simplex*
(Fig. 12, 13; Tables 3, 4)

Diagnosis.—Most bunodont lineage segment of *Hyopsodus paulus*. Slightly smaller in average length of M_2 than *H. paulus-lysitensis*. Compared to all other North American *Hyopsodus* except *H. loomisi*, lower molar trigonid and talonid cusps blunt and unelevated; talonids poorly formed and unnotched. M_3 smaller than in later lineage segments of *H. paulus*. Premolars somewhat longer but less basined than in *H. paulus-lysitensis*. Compared to later *H. paulus*: P_{3-4} hypocristid and hypoconid poorly developed, paraconid more frequently present on M_1 and often on M_2 , metastylid and entostylid more common. M^3 metacone, metaconule, and hypocrista stronger and more distinct than in penecontemporaneous *Hyopsodus loomisi*. Labial and anterior cingula and external ribs of M^{1-3} less developed than in *H. paulus-lysitensis*. In contrast to *H. loomisi*, molar paraconule and protocone elevated above the level of the low anterior cingula. Molar hypocone smaller and more distolabially situated than in *H. paulus-lysitensis*; more robust than in *Hyopsodus loomisi*.

Diagnostic Series.—ACM 2290 (type, *Hyopsodus simplex*), 10108. CM 11478, 12120, 12379, 12404, 28998, 36728, 39427, 57991, 58082, 58093.

Referred Specimens. CM 11464, 11467–11468, 11470, 11478, 12115–12116, 12119–12120, 12185, 12198, 12208, 12224, 12226, 12270, 12273, 12275, 12305, 12344, 12355–12356, 12359, ?12362, 12376–12379, 12382, 12384, 12386, 12404, 12413–12414, 12418, 17466, 34315 (in part), 34373, 34380, 34383, 34391, ?34404, 34415, 34419, 34426, 36118–36119, 36127, ?36131, 36133, 36227, ?36230, 36233, 36235, ?36236, 36237, 36239, 36243, 36246, 36248–36250, 36252, 36548, 36551, 36615, 36617–36620, 36622, ?36623, 36624, 36706–36707, 36710–36711, 36713–36714, 36717–

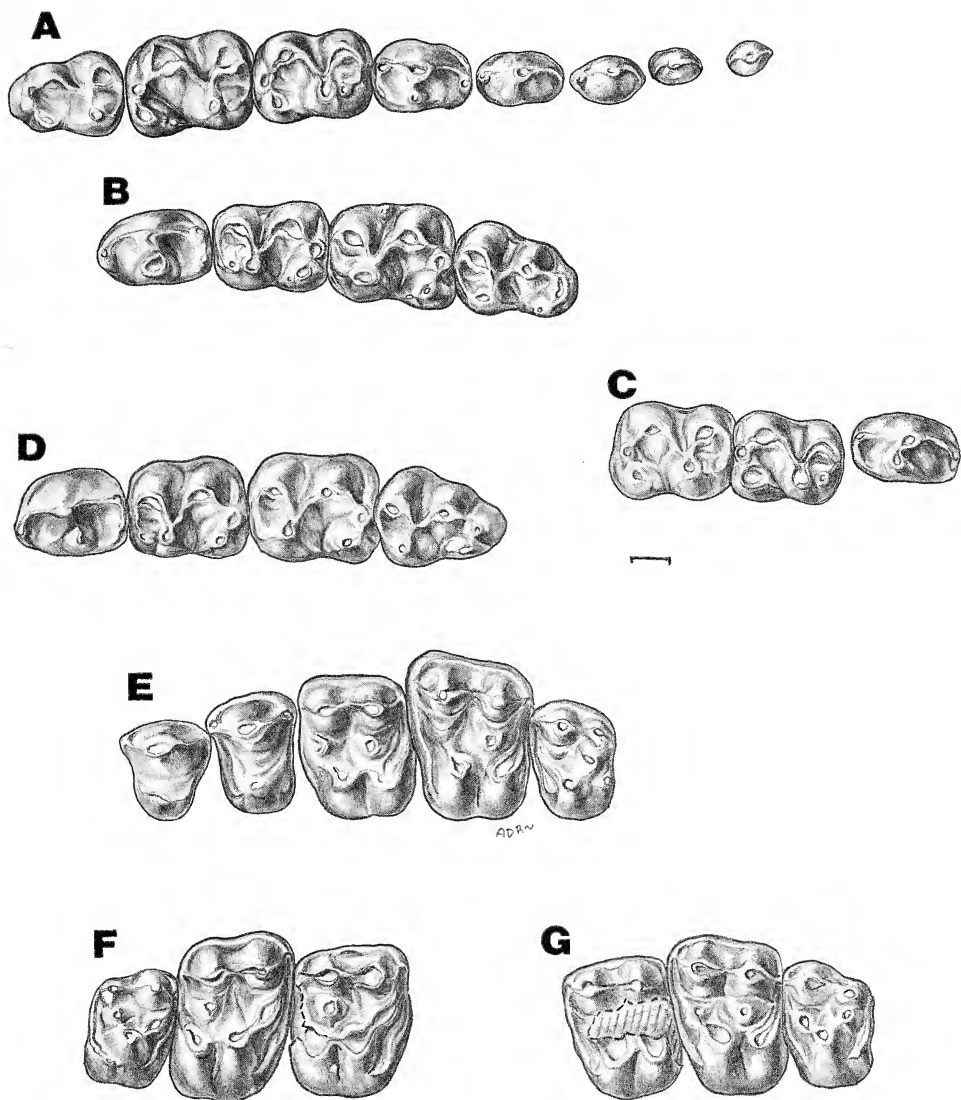


Fig. 12.—Specimens of *Hyopsodus paulus-simplex*. A, CM 12404 (lower); B, CM 58093; C, CM 12376; D, CM 57991; E, CM 12404; F, CM 11478; G, CM 58082. Scale equals 1 mm.

36718, 36720, 36723, 36728–36731, 36733, ?36735, 36742–36746, 36749, 36751–36752, 36756, 39418 (in part), 39420 (in part), 39421 (in part), 39422, 39423 (in part), 39427, 39428 (in part), 39429 (in part), 39430 (in part), 39431, 39432 (in part), 39433 (in part), 39434, 39442 (in part), 39443 (in part), 39444 (in part), 39445 (in part), 39446 (in part), 39447 (in part), 39448 (in part), 39449 (in part), 39450 (in part), 39451 (in part), 39453, 39455, 39456 (in part), 39457–39459, 39460 (in part), 39462 (in part), 39463 (in part), 46646, 51985, ?51987, 51988–51989, 51992, 51994–51998, 53708, 53710, 53713, 53737, 53869, 53913, ?53926, 57955–57956, 57958, 57963, 57991, 58082, ?58083, 58084, 58086, 58088, 58090–58098, 58101, 58107, 58109–58111, 58207–58210, 58213–58214, ?58217, 58220–58221. ACM 2290 (type, *H. simplex*), 6025, 10108, 10294.

Localities.—CM 140–157, 873, 953, Dorsey Creek loc. ACM Tatman Mountain, Clark's Fork Basin Graybull beds.

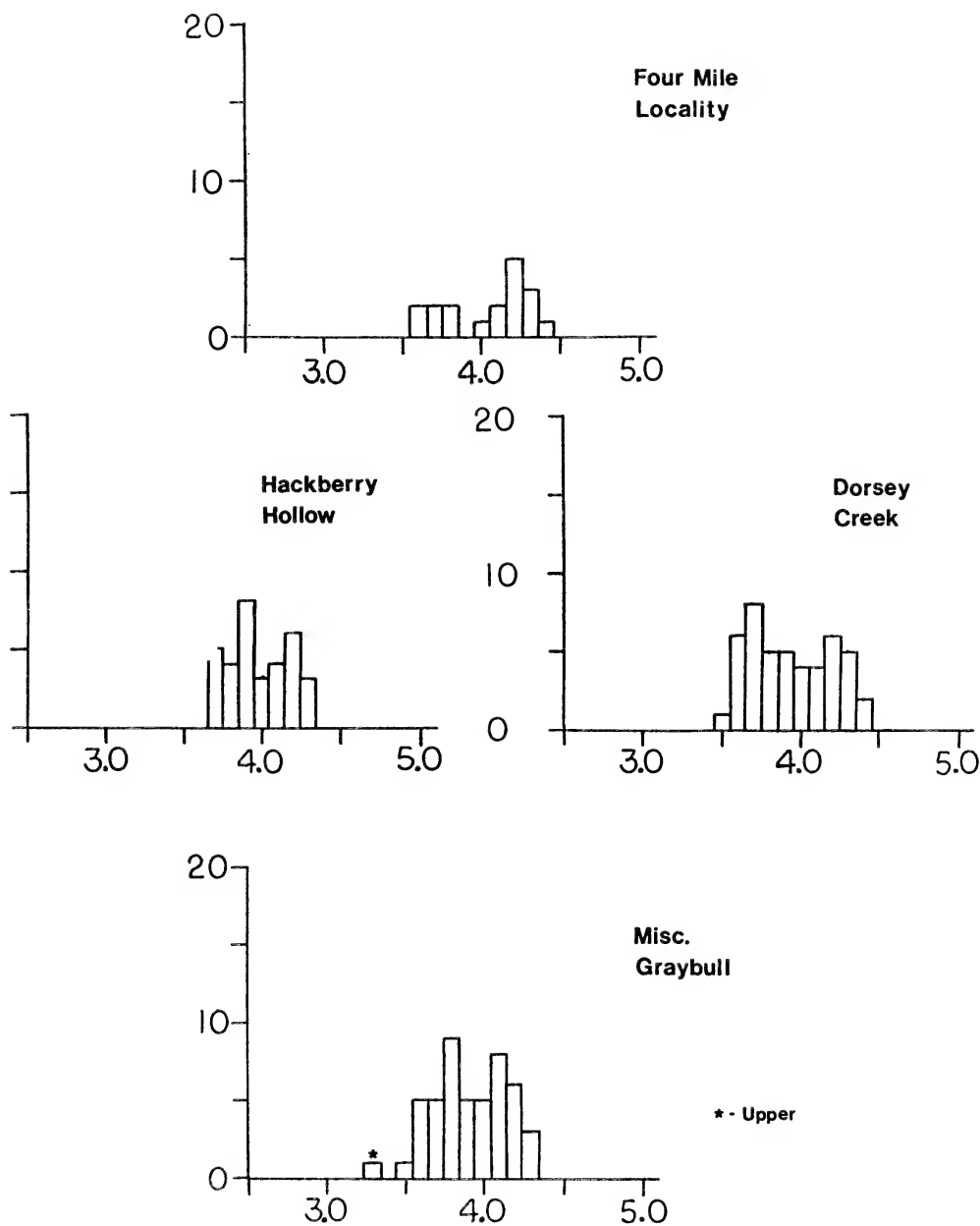


Fig. 13.—Frequency histograms for lower second molars of early Eocene *Hyopsodus*. Four Mile locality is considered earliest Eocene (Sandcouleean), others Graybullian. Vertical axis, number of individuals; horizontal axis, molar length in mm.

Known Distribution.—Sandcouleean through Graybullian of Bighorn Basin and Clark's Fork Basin, Wyoming; earliest Eocene beds of Wasatch Formation, Wasahakie Basin, northwestern Colorado.

Discussion.—The taxonomic status of this lineage segment is based on the

holotype of *H. simplex* (ACM 2290) only; although its specific locality is unknown, it well represents the average morphology of *H. paulus* from the Graybullian Land Mammal Subage. As outlined by McKenna (1960), specimens from the Sand Coulee area referred to *Hyopsodus simplex* by Matthew (1915b) belong to a distinct taxon, *Hyopsodus loomisi*. AMNH 16842, illustrated as *H. simplex* by Matthew, also appears to be a specimen of *Hyopsodus loomisi*. Although confusing, “simplex” is chosen as a segment name here because no other names with formal priority are available; *H. miticulus* is likely to be a more anagenetically progressive form from a distant basin whose type is lost.

Early to middle Graybullian specimens agree in morphology with the type of *H. simplex* and are not as similar to any CM or AMNH dentitions examined from the Almagre and Largo localities of the San Juan Basin (refer to discussion of the concept of species *Hyopsodus paulus*).

Gingerich (1974a) suggested the presence of three lineages of *Hyopsodus* gradually diverging in size in the Graybullian of the Willwood Formation. Data presented here indicates that the two smaller lineages may be delineated based on morphology (compare diagnoses of *H. paulus*–*simplex* with *H. loomisi*). The size divergence of two small to medium-sized taxa noted by Gingerich is possibly confirmed by the much closer clustering of M_2 length between *H. paulus* and *H. loomisi* (the larger representing *H. paulus*–*simplex*) at the comparatively earlier Graybullian CM loc. 873 versus the somewhat later CM Dorsey Creek localities (see Fig. 13). Character overlap is also greater at CM loc. 873; CM 57991 is similar to *H. loomisi* in its poorly differentiated entoconid on M_2 , but otherwise is much closer to the diagnosis of *H. paulus*–*simplex*. Contrary to Gingerich (1989), a slight groove separating the molar protoconid from the metaconid does not distinguish *Hyopsodus loomisi*; it is shared by *H. paulus*–*simplex* and *H. loomisi* and is a function of the larger lingual trigonid area common to all Graybullian and earlier *Hyopsodus*.

Hyopsodus paulus–*simplex* is the most commonly occurring lineage of *Hyopsodus* at most Graybullian localities, but is closely approached in abundance by *Hyopsodus loomisi* at Dorsey Creek and CM loc. 873. Although there is some overlap, *H. paulus*–*simplex* can be recognized by larger average size, a larger, more lingually protruding entoconid on the lower molars, transversely shorter P^{3-4} , and better developed upper molar hypocones and M^3 labial cusps, and labial and anterior cingula. Although its size may be very similar to *H. loomisi*, these characters delineate the segment as early as the Sandcouleean. Primitive characters shared in common with *H. loomisi* include low-crowned cusps on dentitions, poorly developed lophs, cristid obliqua on M_{1-3} meets trigonid more labially, lack of distinct lower premolar anterior and lingual cusp, weak to no basining of P_{3-4} talonid, and small third molars. The high frequency of presence of the lower molar paraconid, sometimes with a distinct base, is also common to Graybullian *Hyopsodus* in general.

One highly variable feature is the shape of the hypoconulid/entoconid on M_3 , which may appear as an arcuate lobe, as two cusps or multiple cusps (as in ACM 16842). In general, the posterior M_3 cusps of *Hyopsodus* specimens are rarely consistent in these types of morphologic detail; “accessory cusps” are common and more probably indicate ontogenetic disturbance (Redline, 1990b). *Diacodexis* shows similar variation (Krishtalka and Stucky, 1985:426). Usually, the length of the tooth and degree of development of the primary cusps are most diagnostically

useful. In *Hyopsodus paulus-simplex*, M_3 is universally short and low crowned, like the type of *Hyopsodus simplex*.

Hyopsodus paulus-simplex is the most primitive known lineage segment of *Hyopsodus paulus*, but appears derived or, alternatively, anagenetically advanced with respect to *Hyopsodus loomisi*. At its first occurrence, it already possesses the larger lower premolars, robust molar entoconids, and more distinct upper molar hypocones and cingula typical of pre-Bridgerian *Hyopsodus*. Were it not for the co-occurrence of both *H. paulus-simplex* and *H. loomisi* in the Sandcoulee and throughout the early to middle Graybullian and upper P^4 differences, *H. loomisi* might simply be considered a most primitive form of *H. paulus*.

Hyopsodus minusculus Leidy, 1873

(Fig. 5, 14; Table 5)

Holotype.—ANSP 10259. Partial LP^4 , LM^{1-3} . Collected from Dry Creek, Bridger Formation, Bridger Basin, Wyoming.

Diagnosis.—Very small size compared to other *Hyopsodus*; mean length of M_2 in the Wind River Basin, 3.5 mm. Compared to *H. paulus-paulus*, M^{1-2} more nearly square; (length/width ratio closer to one); M^1 closer in occlusal area to M^2 ; M^{1-2} paraconule smaller, base not distinct, more confluent with protoloph. Compared to all *H. paulus*, distinctly more ridge-like hypocrista with very small or absent hypocone on M^3 ; hypocrista wraps more anterolingually around protocone base, often approaching or joining the anterior cingulum. External cingula more frequently well expressed on upper premolars and molars; in contrast to *H. paulus-paulus*, often completely wraps around labial margin of teeth. Compared to other Wasatchian or early Bridgerian *Hyopsodus*, P_{3-4} shorter, protocone and hypocristid much higher than lingual margin of teeth. Compared to *H. paulus*, *H. minor*, and *H. powellianus*, P_4 talonid more weakly basined, notched, with no trace of entoconid; paraconid weaker, with preparacristid anteriorly shifted close to protoconid and metaconid somewhat posteriorly placed. Lower molars appear more elongate than in *H. paulus*; M_{1-2} hypoconulid smaller and posteriorly shifted; base of entoconid more closely appressed to hypoconulid. M_{1-3} metastylid and entostylid more rare than in *H. paulus-paulus*. Molar cristid obliqua joins trigonid more labially than in *H. paulus-paulus*.

Diagnostic Series.—ANSP 10259 (type, *Hyopsodus minusculus*). AMNH 12496, 14623. CM 21050, 22339, 27442, 29124, 29128, 30928, 40618, 44916.

Referred Specimens.—CM ?4950, 4951–4952, 21012, 21044 (in part), 21045, 21047, 21050, 21053, 21055, 21061, 21064, 21071–21072, 21077, 21079–21080, 21086–21087, 21090, 21093–21094, 21099–21100, 21102, 21106, 21923, 21926, 22319, 22339–22341, 22343, 22530, 22531 (in part), 27438, 27440–27446, 29123–29124, 29127–29129, 29131, 29135 (in part), 30892, 30894, 30896–30897, 30901–30902, 30905, 30907–30908, 30910–30915, 30918, 30922–30924, 30928–30929, 30934, 31003, 31005–31006, 31009, 31011–31012, 31329, ?35742, 35758–35759, 35761–35770, ?36447, 36448, 36943–36944, 37331 (in part), 37332 (in part), 40080, 40084, 40089–40091, 40093, 40095–40097, 40616, 40626–40628, 40631–40632, 40634–40635, 40637–40639, 40641–40644, 40646, 40648–40649, 40651–40652, 40654, 40656, 40658, 40660, 40663–40664, 40676, 41618, 44916, 44919–44922, 44923 (in part), 44924–44929, 44938, 44941–44943, 44945, 44947–44954, 44956 (in part), 44959, 44961–44962, 44971, 44974 (in part), 44976–44977, 44983 (in part), 44991–44992, 44997, 45166, 45190, 45322–45324, 45958, 45960, 45962, 45965, ?45967, 45971, 46658, 47117–47119, 47223, 47239, 55035, 55039, 55048, 55050, 55052, 55055–55056, 55058, 55061–55062, 55065–55066, 55071, 55073, 55075, 55078, 55080–55081, 55084–55085, 55219–55220, 55223–55224, 55226, 55230, ?55231, ?55232, 55235–55237, 55239, 55242–55245, 55247, 55253–55254, 55257, 55261–55265, 55273, 55275, 55280–55282, 55286–55288, 55290–55291, 55294, 55298, 55302–55303, 55305–55306, 55312–55313, 55315, 55318, 55320–55321, 55323, 55325,

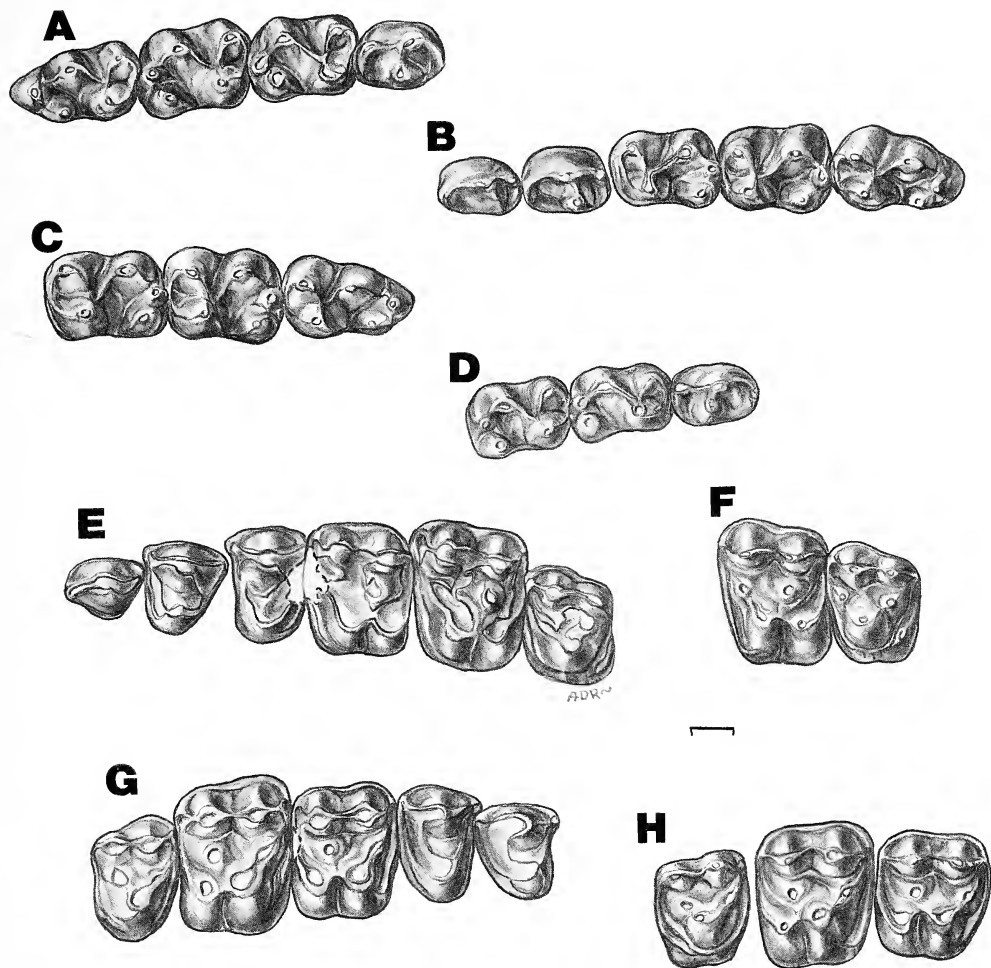


Fig. 14.—Specimens of *Hyopsodus minusculus*. A, CM 21050; B, CM 40080; C, CM 21061; D, CM 36447; E, CM 56236; F, CM 44945; G, CM 22339; H, CM 22339 (separate specimen). Scale equals 1 mm.

55327–55328. UCM 42820, ?42840, ?42868, 42871, 45364, 45537, 45552, 46590. UW 23534, 23536. AMNH 12496, 14612–14613, 14623–14624. ANSP 10259 (type, *H. minusculus*).

Localities.—CM 34, 1036, 1038, 1543, 1545, 1548. UCM 80064, 80065, 81026. UW V89041. AMNH “Lost Cabin Beds”; 4 mi S of Granger, Wyoming, loc. (Blacksforkian). ANSP loc. Dry Creek, Wyoming (Blacksforkian).

Known Distribution.—Earliest Bridgerian (Gardnerbuttean) of Wind River Basin, Wyoming; Huerfano Basin, Colorado; Blacksforkian of western North America.

Discussion.—This marks the first time small-sized *Hyopsodus* from the Wind River Basin (as well as the Gardnerbuttean of the Huerfano) have been referred to *Hyopsodus minusculus*. As in *H. paulus*, *H. minusculus* from the Gardnerbuttean of the Lost Cabin Member is morphologically close to the types and referred specimens from the younger Blacksforkian localities. CM 55236 possesses a P²

Table 5.—Summary of statistics, lower and upper dentitions of *Hyopsodus minusculus*. High, low, mean, SD in mm.

	P ₃ (L, W)	P ₄ (L, W)	M ₁ (L, W)	M ₂ (L, W)	M ₃ (L, W)
High	2.7, 2.0	3.2, 2.6	3.5, 3.0	3.9, 3.3	4.1, 3.1
Low	2.3, 1.6	2.6, 2.0	3.1, 2.3	3.1, 2.5	3.4, 2.2
n	11	43	70	112	72
Mean	2.5, 1.8	2.8, 2.2	3.3, 2.6	3.5, 3.0	3.9, 2.6
SD	0.11, 0.12	0.17, 0.15	0.11, 0.16	0.11, 0.19	0.16, 0.17
CV	4.4, 6.7	6.1, 6.8	3.3, 6.2	3.1, 6.3	4.1, 6.5
	P ³ (L, W)	P ⁴ (L, W)	M ¹ (L, W)	M ² (L, W)	M ³ (L, W)
High	3.0, 3.0	2.8, 3.9	3.8, 4.3	4.0, 5.1	3.2, 4.1
Low	2.2, 2.5	2.3, 3.0	3.1, 3.4	3.1, 4.1	2.5, 3.2
n	6	11	21	29	25
Mean	2.5, 2.6	2.6, 3.4	3.4, 3.9	3.5, 4.5	2.8, 3.7
SD	0.25, 0.35	0.14, 0.24	0.17, 0.21	0.20, 0.23	0.19, 0.26
CV	10.0, 13.5	5.4, 7.1	5.0, 5.4	5.7, 5.1	6.8, 7.0

with a lingually expanded inner surface, somewhat more typical of later *Hyopsodus* (see Gazin, 1968:45) than of Wasatchian lineages. Similar-sized CM 40660 does not feature the lingual expansion, varying toward the primitive condition.

An insufficient number of Blackforkian specimens were examined to allow division of *Hyopsodus minusculus* into successive lineage segments. Specimens from the uppermost Wind River Formation referred to *H. minusculus* share with later Bridgerian material the derived characters listed in the diagnosis. West (1979a) concluded that *H. minusculus* did not survive beyond the time of Bridger B deposition, but noted regional variation in the relative abundance of small specimens from various Blackforkian localities. In earliest Bridgerian sediments of the Wind River Basin, *H. minusculus* is extremely common, identifiable dentitions being as numerous as the intermediate-sized *Hyopsodus paulus*. As will be discussed later, this pattern supports the conclusion that different-sized lineages of *Hyopsodus* were environmentally specific.

Recently, specimens of *H. minusculus* have also been recovered from the southern Wind River Basin in the vicinity of Oil Mountain, Fremont County (UW loc. V89041). Along with associated *H. paulus*, this record supports preliminary observations that the locality is earliest Bridgerian in age (J. Amos, University of Wyoming, personal communication). It also confirms that the occurrence of non-overlapping populations of *H. paulus* and *H. minusculus* marks the onset of the earliest Bridgerian.

Like *H. paulus-paulus*, *Hyopsodus minusculus* appears to be less variable in character expression than comparable Wasatchian species or lineage segments. There is virtually no size (Fig. 6) or morphologic overlap with the Gardnerbuttean or Blackforkian *H. paulus* lineage segment. Overlap, however, does occur with a number of Lostcabinian specimens of *H. paulus-wortmani* (see discussion of lineage segment *H. paulus-wortmani*). For instance, CM 30928 has a well-developed M³ hypocone, more typical of *H. paulus-wortmani*, but one that is part of a strongly developed, anteriorly tracing hypocrista, as in *H. minusculus*. Again, *H. paulus-paulus* shows similar overlap with *H. paulus-wortmani*, suggesting a common origin for both *H. minusculus* and *H. paulus-paulus*.

Hyopsodus minusculus is similar in size to the late Graybullian through Lysitean species *Hyopsodus minor*, but no derived characters (other than overall size)

suggest a relationship between these two small-sized lineages. *Hyopsodus minusculus* shares lophodont molars, shortened premolars, and transversely compressed premolar paracones, among other characters, with lineage segment *H. paulus-wortmani*, while being derived in lower premolar talonid structure and molar shape and structure as detailed in the diagnosis. *Hyopsodus minor* shares primitive features with *Hyopsodus loomisi*, and to a degree with *H. paulus-simplex*, and is distinct in morphology from *H. minusculus*. Additionally, *Hyopsodus minor*, or a suitable intermediate between *H. minor* and *H. minusculus*, is not known from the Lostcabinian of the Wind River Basin, nor apparently from the Willwood Formation Lostcabinian (size data of Gingerich, 1974a).

The pattern of *Hyopsodus* phylogeny suggests that two small *Hyopsodus* lineages, *H. minor* and *H. minusculus*, iteratively diverged in the early Eocene. The first evolved in the early Wasatchian (discussed below) and the second at the close of the Wasatchian.

Hyopsodus minor Loomis, 1905
(Fig. 10, 11, 15; Table 6)

Hyopsodus wortmani minor Matthew, 1915b.

Holotype.—ACM 3492. RM₁₋₃. Collected from Lysite Beds, Wind River Formation, Wind River Basin, Wyoming.

Diagnosis.—Very small size compared to other *Hyopsodus*, smallest species of *Hyopsodus*. Molar conules smaller than in *H. minusculus*. M¹⁻² hypocone small with base restricted in size and more separated from protocone than in other *Hyopsodus*. M³ relatively more square than in *H. minusculus*; hypocrista wide and more posteriorly situated. M³ protocone and axis of trigon centrally located; crown is most anteroposteriorly symmetrical of *Hyopsodus* species. Labial ribs and ectocingula (particularly immediately labial to molar metacone) less distinct than in penecontemporaneous *H. paulus-lysitensis*, better developed than in *H. loomisi* and *H. paulus-simplex*. Differs from *H. minusculus* in having talonids somewhat basined with entoconid on P₄; and with lower premolar metaconids more anteriorly placed. M₁₋₃ paraconid variably present, less common than in other Lysitean *Hyopsodus*. In contrast to other *Hyopsodus* except *H. loomisi*, entoconid and hypoconulid on M₁₋₂ are restricted, with merged bases, and rarely extend more lingually than trigonid. Anterior cingulids of lower molars weaker than in other *Hyopsodus*.

Diagnostic Series.—ACM 3492 (type, *Hyopsodus minor*). CM 9966, 12151, 22699, 39865, 49400, 49415, 49432.

Referred Specimens.—CM 4904, 9779, 9966, 10471–10473, 12151, 12242, 19819, 20941, 22693 (in part), 22699, ?39175, 39185, 39196, 39289, ?39486, 39526, 39529, 39800, ?39820, 39861 (in part), 40692–40693, 45332, 45351, 45370–45371, 45934, 45955, 45976, 45992, 45995 (in part), 45997 (in part), 46815–46816, 46850, 49400, 49408, 49415, 49427, 49430, 49432, 49434, 60567, 60584–60586, ?60587. ACM 2308, 3492 (type, *H. minor*).

Localities.—CM 112, 118, 130, 142, 793, 797, 800, 802, 806, 811, 813, 928, 931, ?936, 1007, 1021, 1025, 1064, 1091, 1903, DeBeque Fm., nonspecific horizon. ACM Lysite Beds (Loomis collection).

Known Distribution.—Late Graybullian through Lysitean of Bighorn Basin, Wyoming; ?late Graybullian/?early Lysitean of Piceance Basin, Colorado, and San Juan Basin, New Mexico; ?early Lysitean through Lysitean of Wind River Basin, Wyoming. ?Late Lysitean/?early Lostcabinian of Wind River Basin, Wyoming.

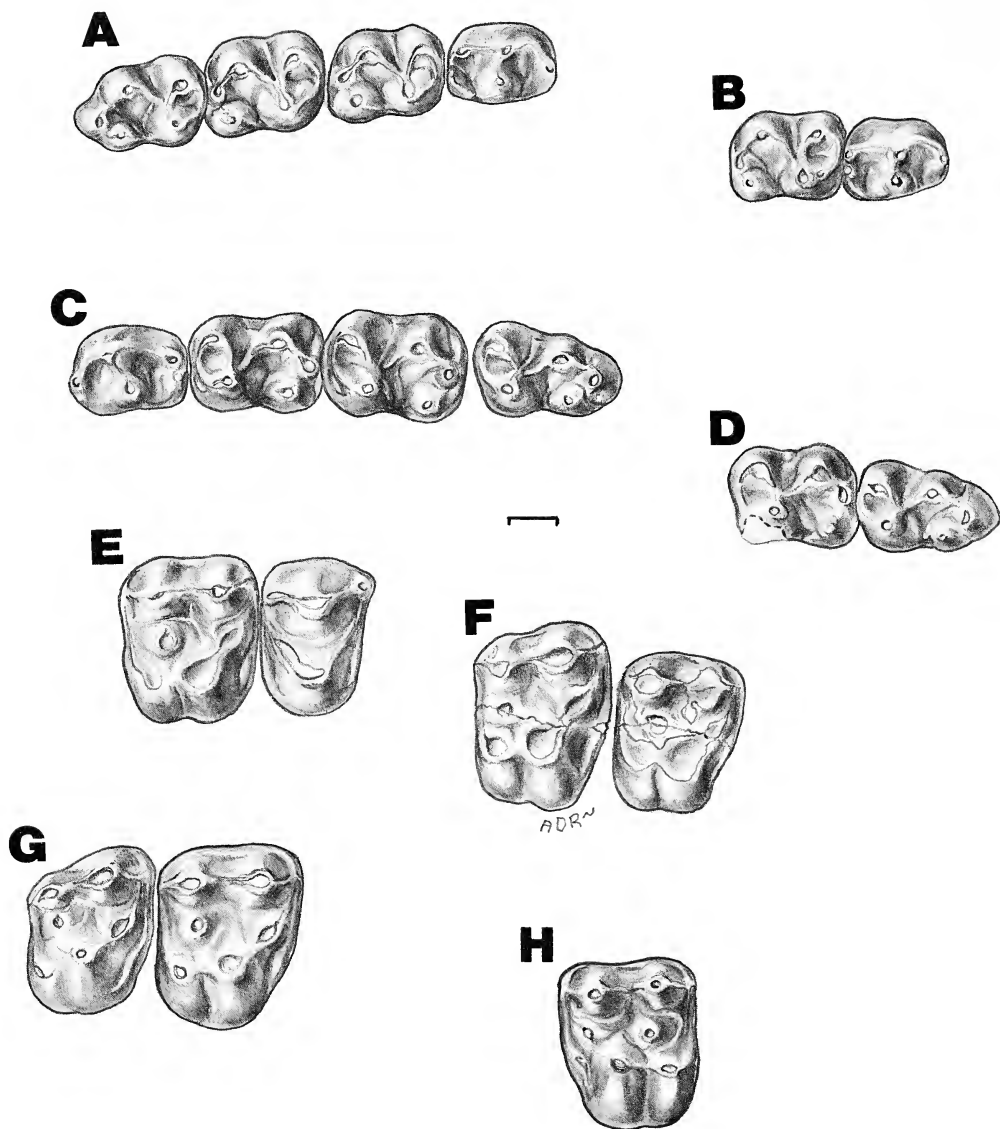


Fig. 15.—Specimens of *Hyopsodus minor*. A, CM 49400; B, CM 22699; C, CM 19819; D, CM 45371; E, CM 22694; F, CM 20941; G, CM 28752; H, CM 28668. Scale equals 1 mm.

Discussion.—*Hyopsodus minor* is a relatively rare constituent of the Lysite fauna of the Wind River Basin but is far more plentiful in the Lysitean of the Bighorn Basin (*H. wortmani* of Gazin, 1968). At the time of Kelley and Wood's (1954) revision, the holotype was the only known specimen. Matthew (1915*b*) referred other material from the AMNH collections to *H. wortmani* ?*minor* but suggested these dentitions showed elongate, high-cusped molars. No specimens with this morphology are present in the very large CM and ACM Lysite Member collections examined for this study. More recent collecting in the Lysite Member has produced new material of *Hyopsodus minor*, enabling a more complete di-

Table 6.—Summary of statistics, lower and upper dentitions of *Hyopsodus minor*. High, low, mean, SD in mm.

	P ₃ (L, W)	P ₄ (L, W)	M ₁ (L, W)	M ₂ (L, W)	M ₃ (L, W)
High	2.7, 2.1	3.2, 2.4	3.3, 2.7	3.4, 3.1	3.7, 2.8
Low	2.4, 1.9	2.6, 1.8	2.9, 2.3	3.0, 2.4	3.4, 2.2
n	3	10	15	16	12
Mean	2.5, 2.0	2.8, 2.1	3.0, 2.5	3.2, 2.7	3.5, 2.4
SD	0.12, 0.09	0.20, 0.16	0.11, 0.11	0.13, 0.17	0.08, 0.16
CV	4.8, 4.5	7.1, 7.6	3.7, 4.4	4.1, 6.3	2.3, 6.7
	P ³ (L, W)	P ⁴ (L, W)	m ¹ (L, W)	m ² (L, W)	m ³ (L, W)
High	— —	3.0, 4.0	3.5, 4.4	3.8, 4.8	3.4, 4.3
Low	— —	— —	3.0, 3.7	2.9, 3.5	2.2, 3.4
n	—	1	6	6	3
Mean	— —	— —	3.3, 4.2	3.4, 4.4	2.9, 3.9
SD	— —	— —	0.17, 0.26	0.32, 0.46	0.54, 0.40
CV	— —	— —	5.2, 6.2	9.4, 10.3	18.6, 10.3

agnosis. The upper dentition is still too incompletely known for confident identification; in fact, the high coefficient of variation for upper teeth of *Hyopsodus minor* (Table 6) indicates that some specimens referred here to *H. minor* might be *H. paulus*. In contrast to the upper dentition, there is less variability in the morphology of lower dentitions of *Hyopsodus minor*. This low level of variation may be attributable in part to the limited number of specimens (a larger number might suggest variation in teeth not well represented by the CM sample) or their restricted geographic provenance. A similar phenomenon is also apparent in the relatively rare *Hyopsodus powellianus-walcottianus* lineage segment discussed later.

Differing from the Lysite Member of the Wind River Basin, *Hyopsodus minor* (Fig. 23) is more common in the San Juan and Piceance basins. In the Bighorn Basin, two specimens (CM 12151 and 12262) from the Willwood Formation bearing labels marked “upper Graybull” closely meet the diagnosis of *Hyopsodus minor*, except for a proportionately smaller M³ in CM 12151. The new species, *Hyopsodus pauxillus* (Gingerich, 1994), reported from the W5 interval of the Clark’s Fork Basin, also fits the *H. minor* size range—with concurrent restriction of the molar talonid that confirms a possible relationship with *H. loomisi* (see below).

Hyopsodus minor is very different from earliest Bridgerian *Hyopsodus minusculus* and *Hyopsodus paulus-wortmani*, which are somewhat similar in size. *Hyopsodus minusculus* possesses shared/derived characters in common with *H. paulus-paulus* and *H. paulus-wortmani* and has shorter, less molariform lower premolars than *H. minor*. *Hyopsodus minor* is biostratigraphically separated from *H. minusculus* in the Wind River Basin (and other basins with a good middle to late Wasatchian record) and does not occur in Lostcabinian horizons, with the exception of CM loc. 936. It does not occur with *H. powellianus-walcottianus* or *H. paulus-paulus*.

Hyopsodus minor is tentatively reported from ?early Lostcabinian CM loc. 936. This marks its only lithosympatric occurrence with *Lambdaotherium*. The specimens (CM 40692, 45934, 45938), with poorly differentiated M₂ entoconids and small M₃ hypoconulid, are closer to *H. minor* than to *H. paulus-wortmani* or *H. minusculus*.

The relationships of this poorly known taxon are unclear. With *Hyopsodus loomisi*, *H. minor* shares small size, a small and posterolabially situated entoconid associated with an indistinct hypoconulid on M_{1-2} , relatively open molar talonids, small upper molar hypocones, and low, conical cusps on all teeth. If these similarities imply close relationship, then in parallel with changes in the *Hyopsodus paulus* lineage, the "*Hyopsodus loomisi/minor*" transition involved the gradual acquisition of relatively larger third molars and more strongly expressed anterior and labial cingula. Gingerich (1974a) has given stratophenetic evidence for a small *Hyopsodus* lineage from the Lysite beds of the Willwood Formation that agrees in size with *Hyopsodus minor* from the Wind River Basin. Alternatively, *Hyopsodus minor* may have had a southern origin completely independent from the Bighorn Basin. Two very small jaws (CM 45976 and CM 60585) from the San Juan Basin Almagre and Largo are similar in molar talonid morphology to *Hyopsodus minor*. Although these specimens are too fragmentary to refer to a new species, they alternatively may represent a new taxon because of their extremely small size (see Fig. 23). Other referred San Juan Basin material is nearly identical to specimens from the Piceance Basin. As mentioned above, *H. minor* is well represented in late Graybullian/early Lysitean levels of the DeBeque Formation of the Piceance Basin.

Hyopsodus loomisi McKenna, 1960
(Fig. 13, 16; Table 7)

Holotype.—UCMP 44781. RP²–M². Collected from beds near Four Mile Creek, Washakie Basin, Colorado.

Emended Diagnosis.—Smaller than other *Hyopsodus*. In contrast to other *Hyopsodus*, transverse width of M^1 equal to or only slightly wider than P^4 . In contrast to *H. paulus-simplex*, labial cingula of premolars and molars very weak or absent, especially in area basal to the cusps (premolar paracone, molar paracone and metacone); anterior cingula of molars weak and not at all anteriorly expanded. M^3 smaller than in all other *Hyopsodus*. Hypocone on M^{1-2} labially situated and not as distinctly separated from protocone as in *Hyopsodus paulus* and larger *Hyopsodus* lineages. Cusps of lower dentition lower crowned and premolars shorter than in *H. paulus-simplex*. Entoconid labially situated, in contrast to other *Hyopsodus* except some *H. minor*, talonid width equal to or less than trigonid width. M_3 very short, posterior cusps often not as separate as those of *H. paulus-simplex*. Paraconid more frequent on trigonid of M_{1-3} than in all other North American *Hyopsodus*.

Diagnostic Series.—UCMP 44781 (type, *Hyopsodus loomisi*). CM 12375, 16751, 51984, 53715, 53893, 57989, 58104.

Referred Specimens.—CM 6428, 11460–11462, 12110, 12121, 12149–12150, 12165, 12171, 12241, 12243, 12262, 12274, 12298, 12346, 12354, 12361, 12363, ?12364, 12375, 12380, 12383, 12385, 12387–12388, 12415, 12417, 16751, 16990, 28998, 34315 (in part), 34403, 36121, 36123–36126, 36128, ?36130, 36132, 36145, 36151, 36222–36223, 36228, 36232, 36234, ?36238, 36240–36242, 36244–36245, 36247, 36249, 36251, 36552, ?36553, 36616, 36621, 36625, 36627, 36712, 36715, ?36719, 36722, 36724–36727, 36732, 36734, ?36736, 36737–36739, 36741, 36747, ?36748, ?36753, 36755, 36757–36761, 37370, 39428 (in part), 39429 (in part), 39430 (in part), 39432 (in part), 39454, 39455 (in part), 39456 (in part), 39461, 39463 (in part), 51983–51984, 51986, 51990–51991, 51993, 53704–53707, 53711–53712, 53715, 53717–53720, 53725, 57957, 57959–57960, ?57962, 57964, 57989–57990, 58085, 58087, 58099, 58102–58106, ?58108, 58211–58212, 58216, ?58218, 58219. ACM 6239, 10096. UC 44781 (type, *H. loomisi*), referred specimens in McKenna, 1960. (Elk Creek

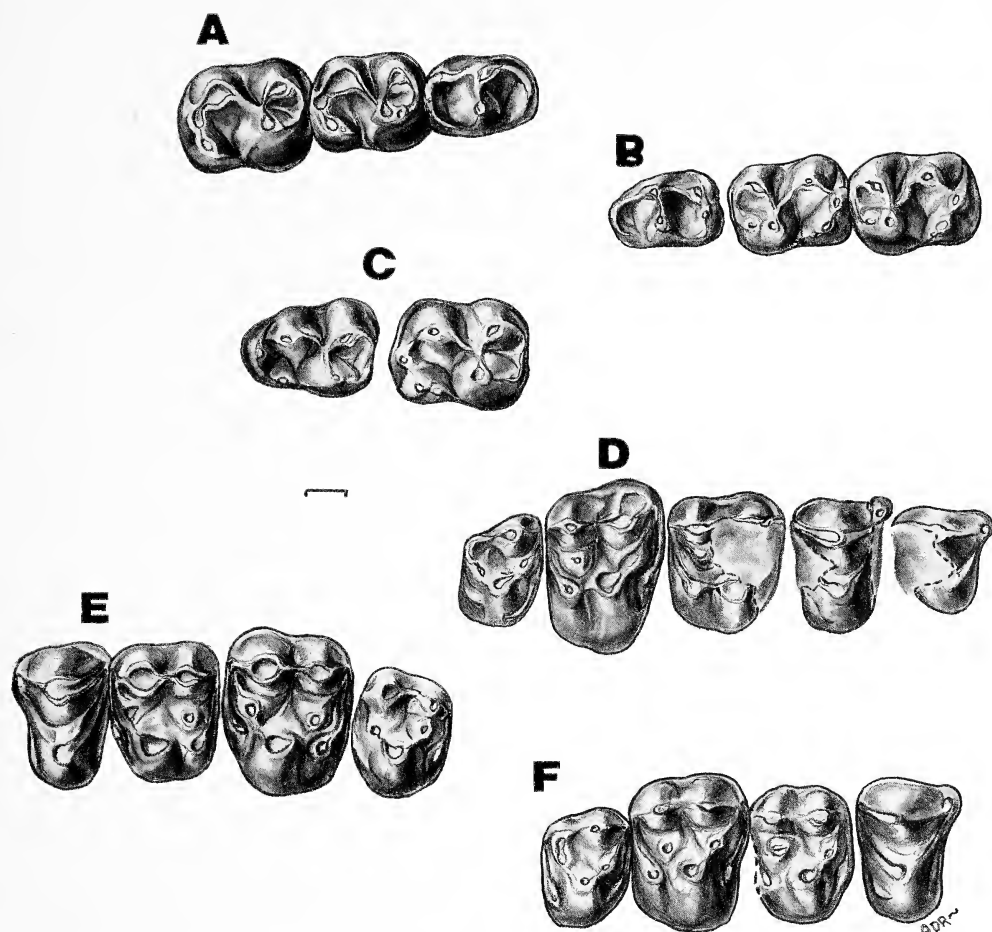


Fig. 16.—Specimens of *Hyopsodus loomisi*. A, CM 51993; B, CM 51984; C, CM 36616; D, CM 53715; E, CM 16751 (left); F, CM 12375. Scale equals 1 mm.

facies, Willwood Fm., tentatively referred). Referred specimens of *Hyopsodus* sp. nov. (Bown, 1979: 102).

Localities.—CM 140–157, 873, 953, Dorsey Creek loc. “*H.* sp. nov. localities” of Bown, 1979. UCMP West Alheit Pocket loc. (McKenna, 1960; partly equals CM loc. 953).

Known Distribution.—Sandcouleean through ?mid-Graybullian of Bighorn and Clark’s Fork basins, Wyoming; earliest Eocene of Wasatch Formation, Washakie Basin, northwestern Colorado.

Discussion.—The portion of the diagnosis concerning the upper dentition of *Hyopsodus loomisi* is essentially unchanged from that of McKenna (1960). Lower molar characters have been added to the diagnosis here. McKenna concluded that lower molar attributes were of no value in discriminating *Hyopsodus loomisi* from *H. miticulus* (= *H. paulus-simplex* here), and discounted Denison’s (1937) remarks concerning differing molar proportions between two possible species. Although the statement “differs in the proportions of the molars” (Denison, 1937:

Table 7.—Summary of statistics, lower and upper dentitions of *Hyopsodus loomisi*. High, low, mean, SD in mm.

	P ₃ (L, W)	P ₄ (L, W)	M ₁ (L, W)	M ₂ (L, W)	M ₃ (L, W)
High	3.0, 2.2	3.4, 2.5	3.9, 3.2	4.0, 3.5	4.1, 3.0
Low	2.5, 1.9	3.0, 2.2	3.3, 2.6	3.5, 2.9	3.4, 2.5
n	5	21	49	62	43
Mean	2.7, 2.1	3.2, 2.4	3.5, 2.9	3.8, 3.2	3.8, 2.8
SD	0.19, 0.10	0.10, 0.10	0.11, 0.14	0.12, 0.15	0.18, 0.14
CV	7.0, 4.8	3.1, 4.2	3.1, 4.8	3.2, 4.7	4.7, 5.0
	P ³ (L, W)	P ⁴ (L, W)	M ¹ (L, W)	M ² (L, W)	M ³ (L, W)
High	3.0, 3.0	3.4, 4.3	3.6, 4.7	3.9, 5.8	3.0, 3.9
Low	— —	2.9, 3.9	3.1, 3.6	3.4, 4.5	2.5, 3.3
n	1	10	21	17	17
Mean	— —	3.1, 4.1	3.3, 4.2	3.7, 5.0	2.6, 3.5
SD	— —	0.14, 0.10	0.15, 0.21	0.16, 0.31	0.15, 0.14
CV	— —	4.5, 2.4	4.5, 5.0	4.3, 6.2	5.8, 4.0

12; citation from McKenna, 1960) is quite vague, two lower molar phena, partly correlated with bimodal size distributions at some localities, are discernible at Sandcouleean and Graybullian localities. Examples include CM 36616 (*H. loomisi*) and CM 57991 (*H. paulus-simplex*) from CM loc. 873, which, although similar in lower molar size, are as dentally distinct as the diagnoses of *H. loomisi* and *H. paulus-simplex*.

Hyopsodus loomisi probably includes Bown's (1979) *Hyopsodus* sp. nov. from the Sand Creek facies of the lower Willwood Formation. Bown mentions shared characters, and the figured specimen is similar to *H. loomisi* in its poorly developed ectocingula, relatively small overall size, and weak, labially situated hypcone on M¹⁻². These Bighorn Basin specimens of *H. loomisi* are tentatively referred here, as they were not examined firsthand.

Graybullian specimens referred to *Hyopsodus loomisi* differ from those from Four Mile (McKenna, 1960) in smaller average size and perhaps more nearly square M¹⁻². Within the Graybullian, *H. loomisi* from CM loc. 873 is larger than that from other CM localities and shows a generally better developed paraconid on M₁₋₃. Stage of evolution in *Hyopsodus loomisi* may account for such differences (and similar differences in the other Wasatchian lineages). Progressively smaller size in *H. loomisi* from successively younger strata is inferred as the norm for this species, but specimens referred to *H. loomisi* exhibit a normal morphologic distribution of the diagnostic characters.

The temporal duration of *H. loomisi* is not precisely known due to a lack of stratigraphic control or coverage for the CM Graybullian specimens. Specimens meeting the diagnostic criteria of this species are recognized at Graybullian CM localities 873, 953, Dorsey Creek, the localities of J. L. Kay (CM), and Elk Creek. If the change in morphology of *Hyopsodus loomisi* proceeded at the same rate as the size divergence noted in the Willwood Formation (Gingerich, 1974a; results of this study, see discussion of *H. paulus-simplex*), then *H. loomisi* may be inferred to span most, if not all, of the Graybullian Land Mammal Subage. There are specimens of *Hyopsodus minor* in the CM Graybullian collections, but *H. minor* never occurs with *Hyopsodus loomisi* at the same locality. Small-sized *Hyopsodus* specimens from the University of Michigan, Yale, and USGS collections, not examined here, may document the pattern of anagenetic change and

geologic range of both taxa. Similarly, analysis of Graybullian *H. paulus* from these collections should improve the systematic resolution of *H. paulus*–*simplex*.

As mentioned previously, *H. loomisi* may be closely related to *Hyopsodus minor*. Lysitean *Hyopsodus minor*, other than being smaller in size, is very close to small *Hyopsodus* from the Piceance and San Juan basins. Together they may comprise a sister group to the more northerly *Hyopsodus loomisi*. Outside of the Bighorn Basin, the Graybullian/Lysitean transition is incompletely known, making hypotheses contrasting cladogenesis, anagenesis, and immigration difficult to assess. More recent faunal analyses of the Willwood Formation (Schankler, 1980; Badgley, 1990; Bown and Beard, 1990) have treated *H. minor* and *H. "loomisi/latidens"* (of Gingerich, 1974a) as representative of the same lineage (see Badgley, 1990:165, table 8). As mentioned above, Gingerich's (1994) *Hyopsodus pauxillus* seems to bridge this gap nicely. These conclusions need further interbasinal correlation for support.

Hyopsodus loomisi, as a discrete morph different from *H. minor*, is limited to the Bighorn/Clark's Fork Basin area (aside from the Four Mile localities of Colorado) and does not persist beyond the Graybullian of western North America.

Hyopsodus powellianus Cope, 1884

Hyopsodus browni Loomis, 1905.

Hyopsodus jacksoni Loomis, 1905.

Hyopsodus lawsoni Loomis, 1905.

Hyopsodus powellianus browni Matthew, 1915b.

Hyopsodus walcottianus Matthew, 1915b.

Holotype.—AMNH 4147, RM₁₋₃. Collected from the Willwood Formation, Bighorn Basin, Wyoming.

Included Lineage Segments.—*Hyopsodus powellianus*–*powellianus*, *H. powellianus*–*walcottianus*.

Diagnosis.—Larger than other *Hyopsodus*; lineage segment *H. powellianus*–*walcottianus* is largest known *Hyopsodus*. Length of P³ approaches or exceeds width and crown is more triangular than in other *Hyopsodus*. Anterior cingula on upper molars, and to a lesser extent on P⁴, broader and more anteriorly expanded than in other *Hyopsodus*. In contrast to *H. paulus*, M³ hypocingula strongly developed and distinctly arcuate, often flares posteriorly; metacone strong but lingually placed in comparison to *H. paulus*. Labial ribs on upper dentition better developed than in *H. minor* and *H. loomisi*. M₁₋₂ hypoconulid larger than in other *Hyopsodus*, with inflated base; molar talonids are more incised than basined. Unlike other *Hyopsodus*, interior talonid margins dominated by inflation of talonid cusps. Unlike other *Hyopsodus* other than *H. paulus*–*lysitensis*, posthypocristid on P₄ strongly developed, often enclosing most of lingual part of talonid basin. Talonid of P₄ comparatively longer than in other *Hyopsodus*, and very rarely notched. Molar paralophid stronger and somewhat more elevated than in other *Hyopsodus*; paraconid usually vestigial, smaller, and structurally does not affect trigonid morphology (as in *H. paulus*). Metastylid as commonly occurring as in *H. paulus*, entostylid more common and comparatively larger.

Referred Specimens.—Listed under individual lineage segments.

Known Distribution.—Lysitean of Buffalo Basin, Wyoming; Lysitean through Lostcabinian of Bighorn Basin, Wyoming; Lysitean through earliest Bridgerian

of Wind River Basin, Wyoming; late Graybullian/early Lysitean of Piceance Basin, Colorado.

Discussion.—Like *H. paulus*, *Hyopsodus powellianus* appears to be an anagenetically evolving lineage. This conclusion is based primarily on the record preserved in the northeastern Wind River Basin and the Bighorn Basin. Large-sized *Hyopsodus* from the more southern basins are not so easily resolved. Specimens that exhibit the diagnostic features of *Hyopsodus powellianus* (near a Wind River Lysitean grade of morphology, see below) are present at the Scenery Gulch locality in the DeBeque Formation. Kihm (1984) noted a *Hyopsodus powellianus* event (first occurrence) in the DeBeque Formation at a higher level, so the Scenery Gulch specimens appear to contradict his immigration hypothesis.

Material approaching the size range of *H. powellianus* occurs in both levels of the San Jose Formation and in the lower levels of the DeBeque Formation. These specimens will be discussed in more detail below as a separate taxon, *Hyopsodus* sp., cf. *H. mentalis*.

In the Wind River Basin, *H. powellianus* exhibits a pattern of morphologic change through time similar to that of the *Hyopsodus paulus* lineage. It is marked by the gradual evolution of dental traits and canalization of these characters in specimens from successively younger sediments. Anagenetic acquisitions are detailed in the lineage segments of *H. powellianus* and include increase in size. There is no shortening of the lower premolar series; both P_3 and P_4 are comparatively elongate and may increase slightly in relative length through time. The lack of plentiful *H. powellianus*–*walcottianus* material makes it difficult to assert this with confidence.

The directional increase in absolute tooth size supports the origin of a large-sized *Hyopsodus* lineage noted by Gingerich (1974a) in the Graybullian and Lysitean levels of the Willwood Formation. In the Wind River Basin, this pattern continues through the mid-Lysitean–Lostcabinian–Gardnerbuttean Land Mammal Subages, much of which are poorly represented or nonexistent in the Willwood Formation. A Graybullian–Lysitean immigration and/or mixing of taxa between the Wind River and Bighorn basins is certainly a strong possibility (discussed below in more detail).

Taxonomic difficulties with this large-sized lineage are not so severe as in other Wasatchian *Hyopsodus* for three reasons. First, the lineage, at least from the Lysitean onward, does not appear to give rise to new taxa. Secondly, the species name is based on a holotype (as compared to the types of *H. miticulus* and *H. mentalis*) collected by Cope from a locality in the Bighorn Basin (not geographically and faunally disjunct from other basins). Additionally, the fossil record is far more complete and controlled by biostratigraphy in the case of *Hyopsodus powellianus* as a taxonomic concept contrasted to that of *H. miticulus* and *H. mentalis* from the San Juan Basin.

Hyopsodus powellianus extends from the Lysitean (Gingerich's [1974a] Bighorn Basin data suggests very probably earlier) through the Lostcabinian of the Wind River Basin and includes *Hyopsodus walcottianus*. It co-occurs with *Hyopsodus paulus*–*lysitensis* and *Hyopsodus minor* in the Lysitean, and *Hyopsodus paulus*–*wortmani* in the Lostcabinian. According to Stucky (1982, 1984a, 1984b), one of the extinctions marking the close of the Lostcabinian was that of *H. walcottianus*. Since 1984, one well-preserved associated dentition of "*H. walcottianus*" (*Hyopsodus powellianus*–*walcottianus* here) has been recovered from the Gardnerbuttean of the Wind River Basin high in the horizons of CM loc. 34. The

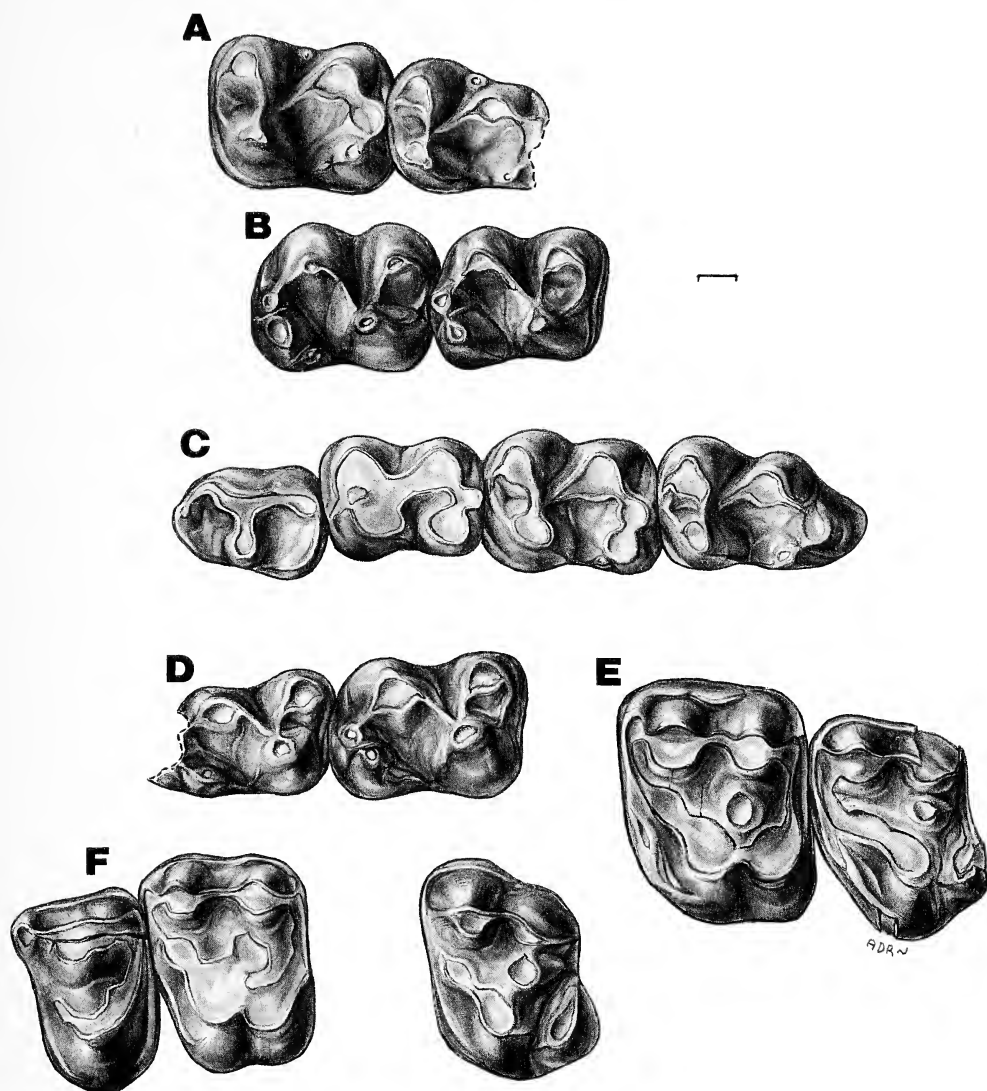


Fig. 17.—Specimens of *Hyopsodus powellianus-walcottianus*. A, CM 45257; B, CM 40668; C, CM 45158 (lower); D, CM 45232; E, CM 40667; F, CM 45158 (upper). Scale equals 1 mm.

biostratigraphic range of this lineage is here formally extended into the earliest Bridgerian.

Lineage Segment *Hyopsodus powellianus-walcottianus*
(Fig. 6, 7, 8, 17; Tables 8, 9)

Diagnosis.—Largest *Hyopsodus* (mean length of lower M_2 , 6.5 mm). More inflated cusps on all molars and premolars. Entostylid on M_{1-3} robust and more common than in all other *Hyopsodus*. Differs from *H. powellianus-powellianus* in having M_{1-2} hypoconulids larger, incompletely separated from entoconids, aligned with entoconids, and large entostylids in plane oblique to anteroposterior

axis of molars. Lower molar metaconids comparatively larger than in other early Eocene *Hyopsodus*, paraconids most completely absent in *Hyopsodus*; trigonids more anteroposteriorly compressed. Protoconids more anteriorly placed relative to metaconids than in *H. paulus*. Anterior cingula of upper molars more expanded than in other *Hyopsodus*, particularly in the area immediately anterior to protocone. M^3 comparatively larger than in lineage segment *H. powellianus*–*powellianus*.

Diagnostic Series.—AMNH 14654 (type, *Hyopsodus walcottianus*), 55247. CM 40667, 45158, 45232.

Referred Specimens.—CM 21220 (in part), 22337–22338, 40667–40668, 45155, 45158, 45232, 45257, 45263, 46472, 49451. AMNH 14654 (type, *H. walcottianus*), 55247.

Localities.—CM 34, 91, 216, 1039, 1040, 1046, Kay's Lost Cabin SE of Riverton loc. AMNH Lost Cabin beds.

Known Distribution.—Lostcabinian through Gardnerbuttean of Wind River Basin, Wyoming. Lostcabinian of Bighorn and Green River basins, Wyoming; Huerfano Basin, Colorado.

Discussion.—*Hyopsodus powellianus*–*walcottianus* is the largest known taxon of *Hyopsodus* (larger than *H. sholemi* of Krishtalka, 1979) and, in the late Wasatchian, may have been ecologically competitive with such herbivores as *Phenacodus vortmani* and *Hyracotherium vassacciense*. However, it is decidedly more rare than either of these taxa in the Wind River Basin. Paleoecologic and taphonomic considerations of Wind River Formation sediments will be discussed in a subsequent section of this report. If *H. powellianus*–*walcottianus* was a larger herbivore occupying a different niche than smaller, penecontemporaneous lineages of *Hyopsodus*, it is not reflected in the morphology of the known tarsal and limb elements, part of AMNH 14654, described and figured by Matthew (1915b). They differ from *H. paulus* in size only.

Overall, the dentition of *Hyopsodus powellianus*–*walcottianus* is quite different from that in other species of *Hyopsodus*. Lower molars especially differ in their talonid cusps. The typical morphology includes a quite enlarged entostylid ("cuspsized" on some specimens such as CM 40668). The entostylid and the entoconid are low crowned and swollen with bases closely appressed. On some specimens, only a shallow groove separates the hypoconulid from the entoconid, which is subequal in size to the hypoconulid.

The range in variation of this lineage segment encompasses specimens such as CM 40668 (above) as well as other specimens (e.g., CM 45257) that, although as large as CM 40668, are not quite as bunodont and somewhat closer to some specimens of *Hyopsodus powellianus*–*powellianus*. This pattern closely approximates that in temporally successive lineage segments of *Hyopsodus paulus*. Other variable characters are: size of lower molar metaconids; angle of the hypoconulid/entoconid cusp plane in relation to the long axis of the tooth; and external cingula on the upper teeth, which can be quite wide and bear cuspules. As in *H. paulus*, the heel of M_3 in the *Hyopsodus powellianus* lineage becomes more distinct and posteriorly extended through time. This is indicated by the longer M_3 of Lostcabinian *H. powellianus*–*walcottianus* compared to Lysitean *H. powellianus*–*powellianus*.

AMNH specimens from the Lostcabinian level of the Huerfano Basin (AMNH 55247 is referred here) appear to be smaller in overall molar size. Aside from somewhat smaller size, these specimens fit the morphologic diagnosis of *Hyop-*

Table 8.—Summary of statistics, lower dentitions of *Hyopsodus powellianus* (lineage segments *H. powellianus*–*walcottianus*, *H. powellianus*–*powellianus*). High, low, mean, SD in mm.

	P ₃ (L, W)	P ₄ (L, W)	M ₁ (L, W)	M ₂ (L, W)	M ₃ (L, W)
<i>H. powellianus</i> – <i>walcottianus</i>					
High	4.8, 3.2	5.5, 4.1	6.4, 4.9	6.5, 5.7	7.8, 5.0
Low	3.8, 2.4	4.7, 3.6	6.0, 4.6	6.4, 5.3	7.2, 4.9
<i>n</i>	2	3	2	4	2
Mean	4.3, 2.8	5.1, 3.8	6.2, 4.8	6.5, 5.5	7.5, 5.0
SD	— —	0.33, 0.22	— —	0.04, 0.15	— —
CV	— —	6.5, 5.8	— —	0.6, 2.7	— —
<i>H. powellianus</i> – <i>powellianus</i>					
High	4.5, 2.8	4.9, 3.6	5.7, 4.5	6.2, 5.3	6.8, 4.7
Low	3.7, 2.4	4.1, 2.8	4.8, 3.6	4.9, 3.9	5.1, 3.4
<i>n</i>	23	79	134	175	159
Mean	4.2, 2.6	4.5, 3.2	5.1, 4.1	5.4, 4.6	5.8, 4.0
SD	0.22, 0.12	0.20, 0.17	0.21, 0.23	0.26, 0.28	0.38, 0.23
CV	5.2, 4.6	4.4, 5.3	4.1, 5.6	4.8, 6.1	6.6, 5.8

sodus powellianus–*walcottianus*. *Hyopsodus powellianus*–*walcottianus* is, so far, unknown from the Gardnerbuttean of the Huerfano.

Lineage Segment *Hyopsodus powellianus*–*powellianus*
(Fig. 10, 11, 18; Tables 8, 9)

Diagnosis.—Larger than most *Hyopsodus* (mean length of M₂ in Wind River Basin, 5.4 mm). Differs from smaller *Hyopsodus* in having large, conical, not compressed or crescentic, cusps on all molars. Less crescentic protocones on P^{3–4} than in *H. paulus*. Hypocone and associated hypocrista of M³ well developed, but differs from other *Hyopsodus* in expanding only in area posterolingual to protocone. Parastyle on P^{3–4} more distinct from paracone than in other *Hyopsodus* species, less anteriorly placed than in *H. powellianus*–*walcottianus*. P⁴ usually more quadrate than in penecontemporaneous *Hyopsodus*. Upper molar anterior

Table 9.—Summary of statistics, upper dentitions of *Hyopsodus powellianus* (lineage segments *H. powellianus*–*walcottianus*, *H. powellianus*–*powellianus*). High, low, mean, SD in mm.

	P ³ (L, W)	P ⁴ (L, W)	M ¹ (L, W)	M ² (L, W)	M ³ (L, W)
<i>H. powellianus</i> – <i>walcottianus</i>					
High	— —	4.9, 6.5	5.6, 7.6	6.7, 8.5	5.8, 7.5
Low	— —	4.3, 6.1	— —	— —	5.3, 7.5
<i>n</i>	—	2	1	1	2
Mean	— —	4.6, 6.3	— —	— —	5.6, 7.5
SD	— —	— —	— —	— —	— —
CV	— —	— —	— —	— —	— —
<i>H. powellianus</i> – <i>powellianus</i>					
High	4.5, 4.8	4.5, 5.7	5.2, 6.6	6.1, 7.7	5.1, 6.5
Low	3.7, 3.7	3.6, 4.6	4.5, 5.6	4.6, 6.1	3.8, 5.2
<i>n</i>	20	35	37	50	43
Mean	4.1, 4.1	4.1, 5.2	4.9, 6.1	5.2, 7.1	4.2, 5.8
SD	0.23, 0.27	0.17, 0.24	0.16, 0.28	0.29, 0.40	0.26, 0.34
CV	5.6, 6.6	4.1, 4.6	3.3, 4.6	5.6, 5.6	6.2, 5.9

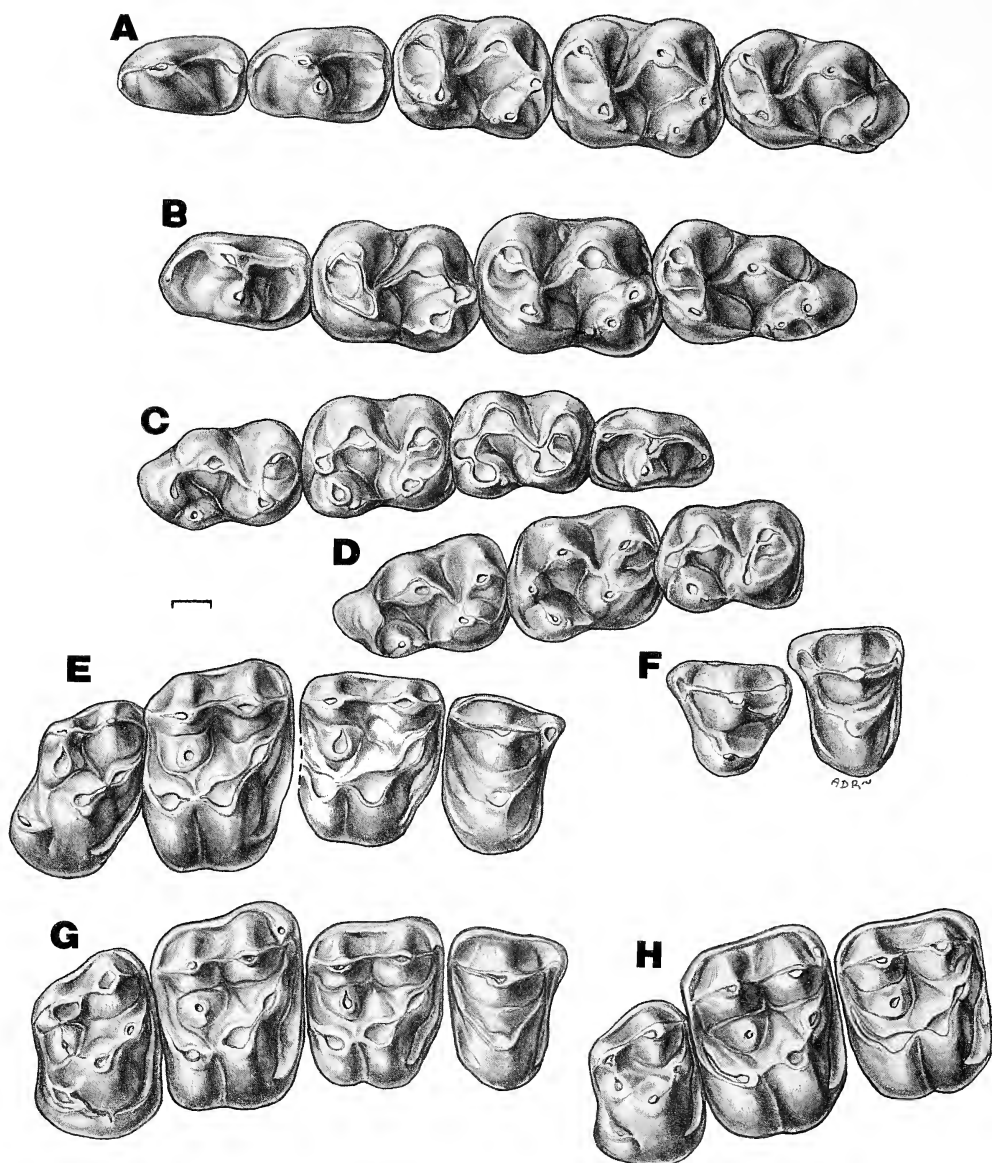


Fig. 18.—Specimens of *Hyopsodus powellianus-powellianus*. A, CM 53829; B, CM 39975; C, CM 19834; D, CM 39790; E, CM 22729; F, CM 54191; G, CM 39508; H, CM 35893. Scale equals 1 mm.

cingula stronger than in *H. paulus*, but not as lingually prominent as in *H. powellianus-walcottianus*. Lower premolar paraconids more anteriorly placed on most specimens than in *Hyopsodus paulus-lysitensis* and *H. minor*. Differs from other *Hyopsodus* (except *H. powellianus-walcottianus*, which further exaggerates these features) in: lower molar metaconid large and tall, and metastylid variable. Paraconid very infrequent and always small, if present. Molar trigonids more anteroposteriorly compressed than penecontemporaneous *Hyopsodus*. M_{1-2} hypocon-

ulid and entoconid enlarged, close to one another on most specimens; entostylid common. Hypoconulid lobe of M_3 very large and well separated from entoconid.

Diagnostic Series.—AMNH 4147 (type, *Hyopsodus powellianus*). ACM 3232 (type, *Hyopsodus browni*). CM 4915, 19834, 22729, 39139, 39167, 39168, 39759, 39975, 53829.

Referred Specimens.—CM 4915, 9924, 15781, 19809–19810, 19812–19815, 19816, 19817, 19820–19822, 19824, 19826, 19832, 19834–19835, 19838, 19840, 19842–19847, 19849, 19851 (in part), 19868, 19880, 20877, 20882, 20890, 20919, 20926, 20943 (in part), 21795–21796, 21891–21892, 21900, 21905–21906, 21911–21912, 21916, 22705–22706, 22711, 22714, 22716, 22718 (in part), 22721–22724, 22727, 22729–22732, 22734 (in part), 22735 (in part), 22736 (in part), 28650–28651, 28656, 28664, 28666, 28667 (in part), 28668 (in part), 28670 (in part), 28671 (in part), 28672 (in part), 28729–28730, 28732, 28734–28736, 28749–28751, 28757–28758, 28760, 28762–28763, 28765, 28767–28769, 28771–28773, 28774 (in part), 28775–28776, 28777 (in part), 28778, 28792–28794, 28936 (in part), 29186–29190, 29196 (in part), 34477, 35887–35888, 35890, 35892, 35894–35895, 35898–35899, 35900–35903, 35906, 35908, 35961, 36069–36070, 36072 (in part), 36072–36073, 36100 (in part), 36101 (in part), 36102 (in part), 36103 (in part), 37057 (in part), 37058, 37059 (in part), 37060 (in part), 37067, 37069 (in part), 37070, 37071 (in part), 39139, 39141–39147, 39149–39152, 39153–39157, 39159, 39165–39168, 39170, 39173–39174, 39177, 39179–39180, 39184, 39188–39189, 39191, 39193, 39214–39216, 39232, 39234, 39229, 39236, 39242–39243, 39278, 39284–39285, 39287–39288, 39292, 39470, 39499, 39501–39503, 39505–39508, 39518 (in part), 39520–39525, 39527–39528, 39530, 39532–39535, 39536–39539, 39541–39542, 39544–39547, 39549, 39551–39557, 39558, 39560–39562, 39564–39566, 39568, 39570 (in part), 39571, 39573–39575, 39661–39662, 39664–39666, 39672, 39750–39751, 39757, 39759–39760, 39789 (in part), 39791, 39795–39797, 39798 (in part), 39802, 39806–39811, 39813, 39816, 39818, 39821 (in part), 39824 (in part), 39826–39829, 39831–39833, 39836, 39839, 39842–39847, 39849, 39851, 39853–39856, 39858–39860, 39861 (in part), 39862, 39864, 39866–39870, 39897, 39900, 39931, 39973–39976, 39980 (in part), 45306, 45308, 45312, 45316–45317, 45319–45320, 45331, 45336–45338, 45343, 45346, 45349, 45352, 45356, 45364–45365, 45367–45369, 45372, 45374, 45377, 45378, 45380, 45383 (in part), 45385–45387, 45392–45395, 45397–45399, 45901, 45907, 45909–45911, 45913, 45916–45917, 45919, 45922, 45927, 46427, 46473–46474, 46477, 46480–46481, 46484–46485, 46487–46490, 46499, 46592, 47262, 47266–47268, 49401–49403, 49405–49407, 49409–49410, 49412–49414, 49417–49420, 49423–49424, 49480–49481, 49484–49485, 49488, 49491–49499, 53795–53796, 53798, 53800, 53802, 53806, 53809–53810, 53812–53815, 53818–53821, 53823, 53825–53826, 53829, 53831, 53833, 54095–54096, 54100, 54108–54110, 54112–54115, 54117–54118, 54120–54121, 54174–54175, 54179–54182, 54185–54187, 54191, 54194–54196, 54198, 54201–54202, 60199–60201, 60203–60205. AMNH 4147 (type, *H. powellianus*), 15015, 15613–15614, 15616. ACM 3232 (type, "*H. browni*"), 3246 (type, "*H. jacksoni*").

Localities.—CM 111–112, 114, 118, 130, 793–794, 797, 800, 801–803, 805–807, 809–813, 877, 927–931, 964–966, 1007–1009, 1064, 1091. ACM Lysite localities. AMNH Bighorn Basin Lysite.

Known Distribution.—Lysitean of Wind River, Bighorn, and Green River basins, Wyoming; Piceance Basin, Colorado.

Discussion.—*Hyopsodus powellianus-powellianus* is extremely common in the Lysite Member of the Wind River Basin where it exceeds *H. paulus-lysitensis* in numbers in most instances.

Measurement data from some localities (Fig. 10, 11) indicate that large specimens of *Hyopsodus* from the Lysite Member, when grouped together, show a higher coefficient of variation and a bimodal distribution in size of M_2 . Loomis (1905), noting size and character differences among a limited number of specimens, named four species of large *Hyopsodus* from the Lysite Member. Matthew (1915b) synonymized these species as the subspecies *H. powellianus browni*. This indicated that the entire Wind River collection was on average smaller than *Hyopsodus powellianus* from the Bighorn Basin. Kelley and Wood (1954) strengthened these conclusions but abandoned the subspecies *browni*. The Lysitean histograms

reported here might also be interpreted as bimodal or even trimodal (Fig. 10, 11) in the length of M_2 . However, the coefficients of variation (Tables 8, 9) are not larger than expected of one taxon (absolute values close to the somewhat smaller *Diacodexis secans-secans* of Krishtalka and Stucky, 1985).

Hyopsodus powellianus from the Bighorn Basin is larger in mean size, but the largest specimens from the Wind River Basin approach it in size. Bighorn Basin material of *H. powellianus* is similar in premolar and molar morphology to the Wind River Lysite *H. powellianus-powellianus*, and aside from average size considerations, these forms are virtually identical. Much of the bimodality in this study is correlated with specific localities; for example, specimens from CM loc. 928 and CM loc. 803 are larger. Localities such as CM loc. 806 and CM loc. 931 have slightly bimodal size distributions, but specimens of *Hyopsodus* show an even distribution of characters that are not positively correlated with the size of the specimen. Plots of M_2 length of specimens from individual Lysite Flats localities (Fig. 19) indicate either no change or a slight increase in average size through time. However, no real trend is apparent; CM loc. 118 and CM loc. 797 (Davis Draw) are upsection from the Lysite Flats localities but specimens are on average somewhat smaller, whereas CM Cedar Ridge specimens are also stratigraphically higher and are uniformly larger. It seems at least possible that slightly different-sized populations of upland and lowland *Hyopsodus powellianus* could have occupied the northeastern margin of the basin in Lysitean times, perhaps with periodic immigration of the even larger individuals from the Bighorn Basin area to the north. The cladogenesis of a large taxon more closely related to *Hyopsodus powellianus-walcottianus* may already have occurred by the Lysitean, perhaps in the Bighorn Basin. These small scale "cladogenetic" events, possibly most common in areas of heterogeneous paleoenvironment, may be responsible for the observed evolutionary pattern of many Eocene taxa. Morphologically, the presence of two very similar populations of *Hyopsodus* cannot be documented, except that the ratio of M_2 to M_1 length is usually higher in the smaller Wind River Lysitean specimens. Analysis of Bighorn Basin material might indicate whether or not further distinctions are valid.

Some of the variable characters of *H. powellianus-powellianus* are the size of the common accessory stylids of the lower molars, degree of paraconid expression (it is never prominent), proximity of the entoconid to the hypoconulid, degree of P_{3-4} talonid enclosure and expression of entoconid on the enclosing posthypoconulid of P_4 , strength and robusticity of premolar and molar paracones, extent of posterior flaring of the hypocrista of M^3 , and various aspects of the labial and lingual cingulids associated with the hypoconulid heel of M_3 .

Examples illustrating the variability in this *Hyopsodus* lineage include CM 39975 and CM 53829, which approach *H. powellianus-walcottianus* in molar talonid structure, and CM 39759, which has a smaller entoconid and more discretely distinct hypoconulid on M_{1-2} , but otherwise is nearly identical to CM 39975 and CM 53829 in premolar structure and size. It is inferred that many of the diagnostic characters of *H. powellianus-walcottianus* are the result of canalization of structures variably distributed in the biostratigraphically older *H. powellianus-powellianus* lineage segment. This was accompanied by an increase in size if the transition was a within-basin anagenetic event, or a less significant size increase if the immigration of larger individuals from the Bighorn Basin was involved.

The distribution of characters within *Hyopsodus powellianus-powellianus* is

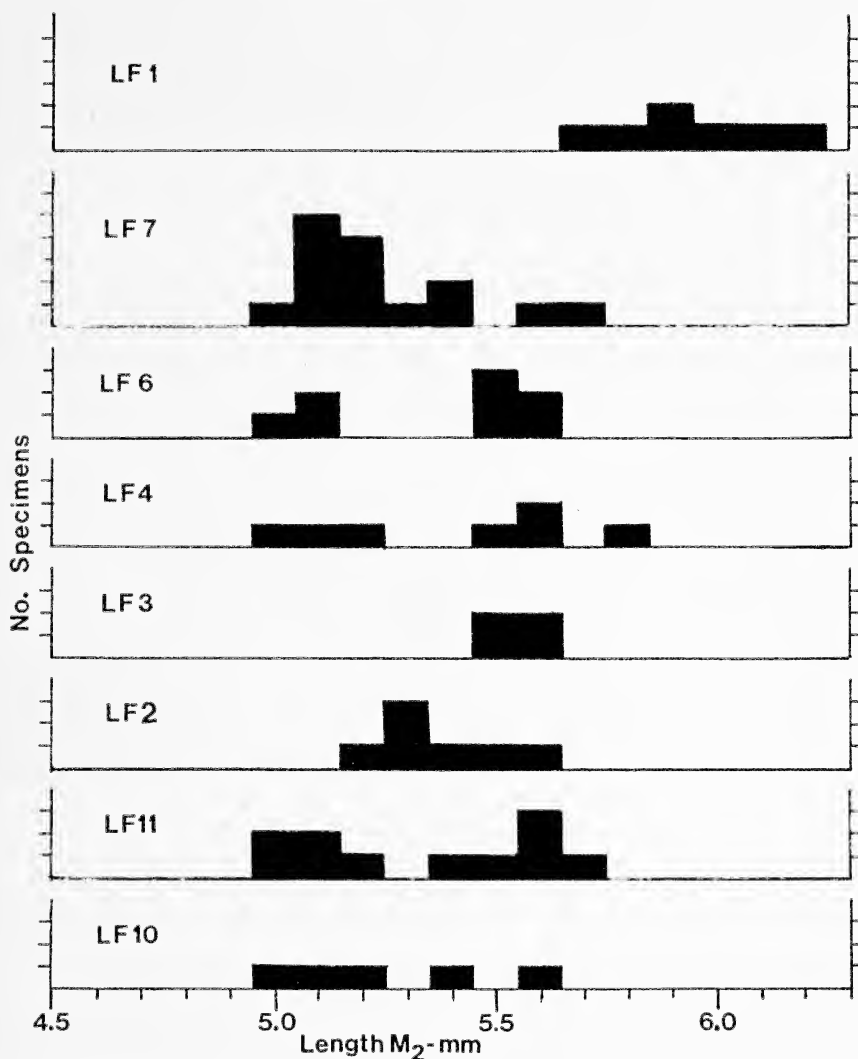


Fig. 19.—Histogram plots of lower second molar lengths of large *Hyopsodus* from Wind River Formation Lysite Flats localities. Localities are positioned in relative stratigraphic order from bottom to top.

noticeably different from that in the other large early Wasatchian form recognized here, *Hyopsodus* sp., cf. *H. mentalis* (below). Isolated upper molars of the two may be difficult to discriminate, but lower premolar and molar trigonid characters as well as a different frequency distribution of molar talonid features seem to distinguish them. These two taxa of *Hyopsodus* do not occur at the same locality, at least in the Wind River Basin.

In the Piceance Basin (Scenery Gulch loc.), one specimen (CM 4915, LP³–M³ [Fig. 23]; RP³–M²) is very close in morphology (more occlusally triangular P³; posteriorly splayed hypocingula) to *Hyopsodus powellianus*–*powellianus* and is assigned to this lineage segment. This specimen is from a locality below the beds

designated by Kihm (1984) as marking the first occurrence of the species *H. powellianus*. From this locality, however, other specimens referred here to *H. paulus-lysitensis* may represent the *H. sp.*, cf. *H. mentalis* taxon discussed below.

As discussed later in this report, the extreme abundance of *Hyopsodus powellianus-powellianus* compared to the rarely occurring *H. powellianus-walcottianus* may be interesting when viewed from a paleoecological perspective.

Hyopsodus sp., cf. *H. mentalis* (Cope, 1874; Matthew, 1915b)
(Fig. 20, 21, 22; Table 10)

(This taxon includes the topotype of *H. mentalis*, some referred *H. mentalis*, the type of *H. lemoinianus* [Cope, 1882b] and various material previously referred to *H. powellianus* and *H. miticulus*.)

Diagnosis.—Intermediate in size between *H. paulus* and *H. powellianus*, larger than *H. paulus* lineage at penecontemporaneous localities. P₄ talonid somewhat shorter than *H. powellianus-powellianus*; entoconid much more distinct, hypo-cristid weaker, does not extend anterolingually to base of metaconid. Molar trigonid not compressed and metaconid less elevated than in *H. powellianus-powellianus*, paraconid more common and larger. Bases of lower molar entoconid and hypoconulid not inflated, cusps usually connected by stronger crest than in most other *Hyopsodus*. Metastylid and entostylid more common than in *H. paulus* and *H. powellianus*; entostylid smaller and more distinct from entoconid base as in *H. paulus*, unlike the cusp-like morphology of *H. powellianus*. Upper molar metacone and paracone less conical, anterior cingula less expanded and hypocone larger and more distinct than in *H. powellianus-powellianus*.

Morphologic Series.—AMNH 4139 (type, *Hyopsodus lemoinianus*), 16194 (topotype, *Hyopsodus mentalis*), 16197. CM 14929, 45946, 46913, 47128, 60565.

Referred Specimens.—(San Jose Formation) CM 14929, 44856, 45983–45985, 45989–45991, 45993, 46862, 46899, 46909, 46913, 46923, 46931, 60564–60566, 60570, 60571, 60572, 60573–60574. AMNH 3307, 16194 (topotype, *H. mentalis*) 16197, 16202, 16304, 86283, 86293. (Wind River, ?early Lysite) CM 45928, 45996 (in part), 45997 (in part), 47011. (Wind River, ?Lysite/?Lost Cabin) CM 34885 (in part), 36451, 40694–40695, 45933, 45936–45937, 45939, 45940–45954, 45957, 45973, 47128, 47912. (Bighorn Basin, Lysite) AMNH 4139 (type, *H. lemoinianus*).

Localities.—CM 858, 936, 1049–1051, 941, 945, 1017–1019, 1021, 1025–1027, 1030–1031, 1033, 1049–1051, 1903–1904, 1907, 1952. AMNH San Juan Basin localities; Bighorn Basin Wasatchian beds (Lysite level).

Known Distribution.—?Late Graybullian/?early Lysitean of San Juan Basin, New Mexico. ?Lysitean of Wind River Basin and Bighorn Basin, Wyoming. ?Late Lysitean/?early Lostcabinian of Wind River Basin, Wyoming.

Discussion.—This is easily the most tenuous grouping of *Hyopsodus* material in this review and should be tested by more detailed comparison of specimens from the San Juan, Bighorn, and Wind River basins. Wind River specimens referred to this taxon show close affinities to the type of *H. lemoinianus* (subsumed in *H. miticulus* by Gazin, 1968) from the Bighorn Basin and large specimens from the Piceance and San Juan basins (probably what Cope intended as *H. mentalis*). Improved biostratigraphic resolution may resolve the relationships of this taxon. Certain primitive but consistent characters and larger size ally the referred specimens for the present time. Its presence as a discrete taxon is indicated by its morphologic distinction from the *Hyopsodus paulus* lineage in the ?early Lysitean of the Wind River Basin at CM localities 1903 and 1904, in the ?early Lostca-

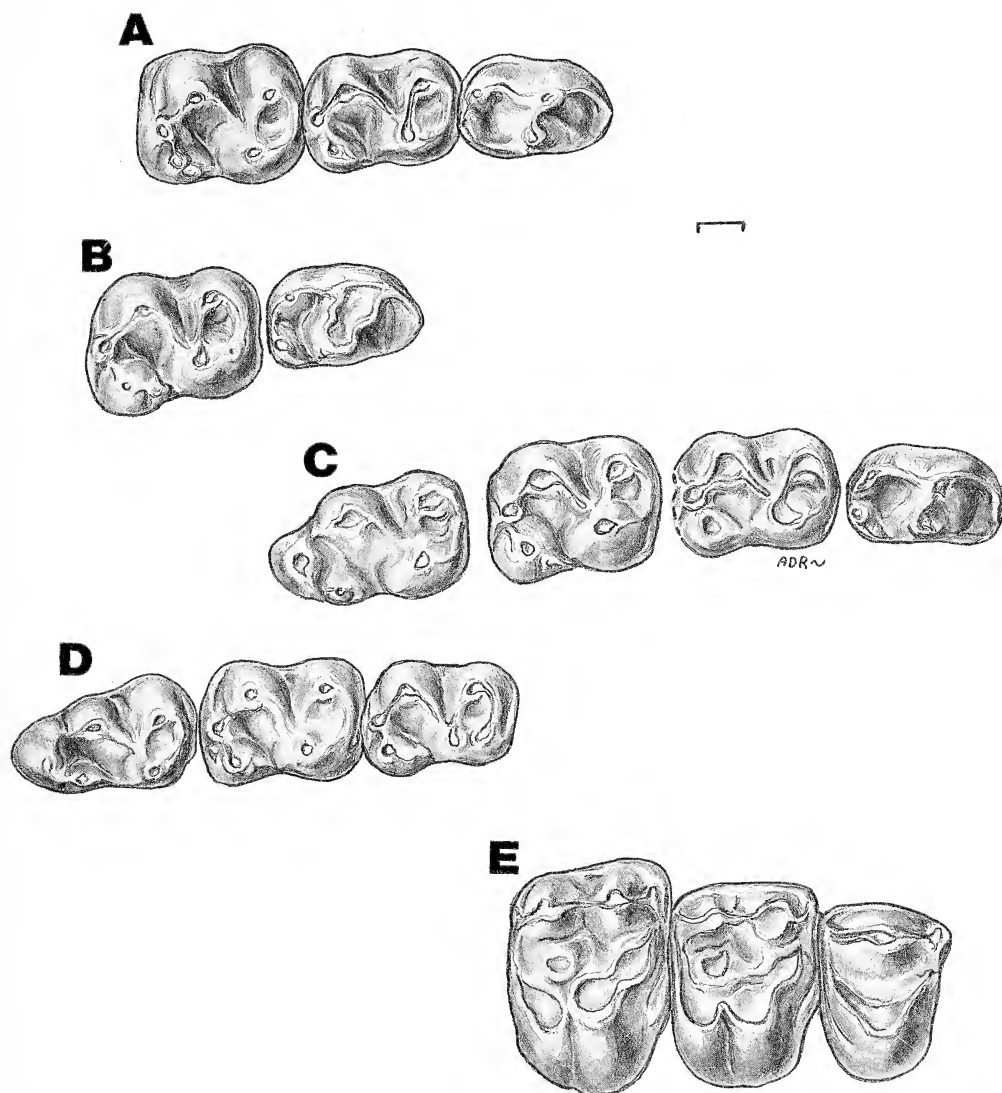


Fig. 20.—Specimens of *Hyopsodus* sp., cf. *H. mentalis*. A, CM 14929; B, CM 47128; C, CM 62663; D, CM 46843; E, CM 62668. Scale equals 1 mm.

binian of the Wind River Basin at CM loc. 1952 and Okie Trail localities, and with “*H. miticulus*” (*Hyopsodus paulus-lysitensis*) in the San Juan Basin.

The holotype of *Hyopsodus mentalis*, collected and described by Cope (1875) from the San Juan Basin, was lost at least as early as Matthew’s (1915*b*) revision. Matthew designated a topotype from the Largo deposits of the basin and synonymized *H. lemoinianus* (Cope, 1882*a*; AMNH 4139) from the Bighorn Basin with this taxon. Gazin (1968), by synonymizing *Hyopsodus mentalis* with *H. miticulus*, essentially removed this material from systematic consideration. Reexamination of these specimens and the CM San Jose Formation collection has disclosed a number of similarities between the *H. mentalis* topotype and the *H. lemoinianus*

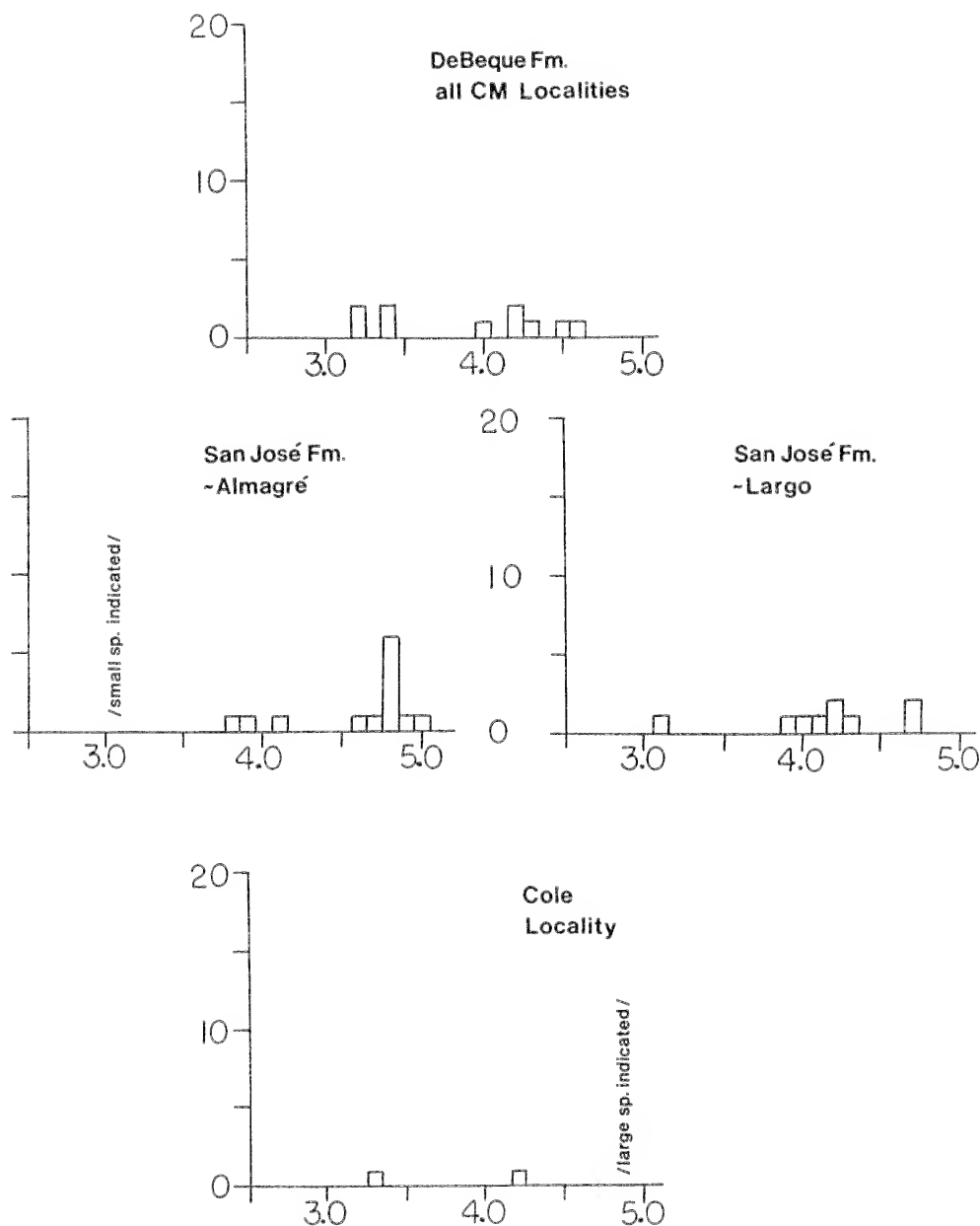


Fig. 21.—Frequency histograms for lower second molars of *Hyopsodus* from ?late Graybullian/?early Lysitean localities from various basins. Cole locality is in the eastern Wind River Basin. Vertical axis, number of individuals; horizontal axis, molar length in mm.

type that are not shared to the same degree by “*Hyopsodus miticulus*” (considered *H. paulus* here). *Hyopsodus lemoinianus* and *H. mentalis* feature more rectangular P_4 and P_3 (but strong entoconid on P_4 of *H. lemoinianus*); a comparatively broader posterior dimension to P_4 ; larger size of the lower molars, and inflated first and

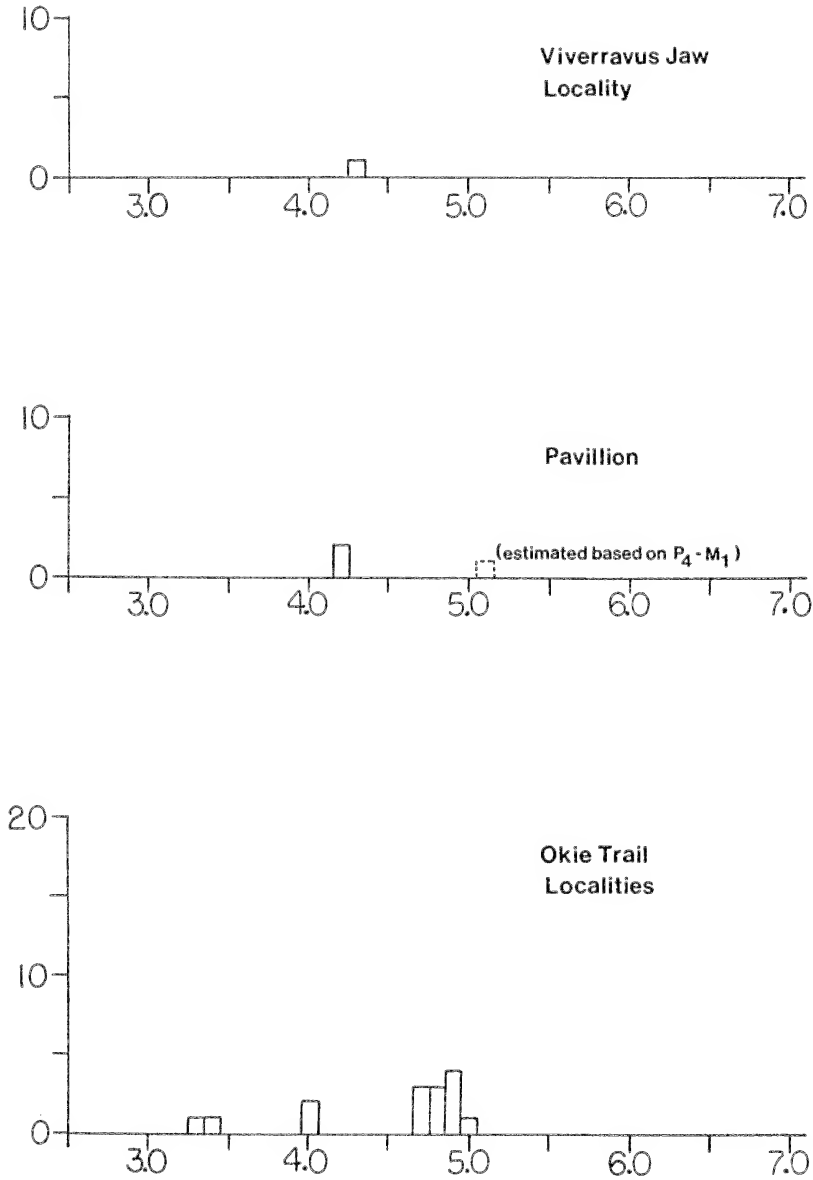


Fig. 22.—Frequency histograms for lower second molars of *Hyopsodus* from ?early Lostcabinian localities in the Wind River Basin. Vertical axis, number of individuals; horizontal axis, molar length in mm.

second molar hypoconulids. *Hyopsodus* sp., cf. *H. mentalis* appears to be intermediate between *Hyopsodus paulus* (M³ and P⁴ morphology, well-separated entoconid/hypoconulid bases) and *Hyopsodus powellianus* in many characters and may be closely related to either of these species.

Hyopsodus sp., cf. *H. mentalis* seems to be absent from the Lysite Member of the Wind River Formation. However, these rocks outcrop only in the immediate

Table 10.—Summary of statistics, lower and upper dentitions of *Hyopsodus* sp., cf. *H. mentalis*. High, low, mean, SD in mm.

	P ₃ (L, W)	P ₄ (L, W)	M ₂ (L, W)	M ₂ (L, W0)	M ₃ (L, W)
High	3.7, 2.5	4.3, 3.3	4.9, 4.1	5.0, 4.5	5.8, 3.5
Low	3.4, 2.4	3.7, 2.7	4.3, 3.3	4.6, 3.9	4.7, 3.3
<i>n</i>	8	19	22	23	17
Mean	3.6, 2.4	4.0, 2.9	4.5, 3.6	4.8, 4.1	5.2, 3.4
SD	0.12, 0.04	0.15, 0.16	0.18, 0.20	0.10, 0.16	0.25, 0.08
CV	3.3, 1.7	3.8, 5.5	4.0, 5.6	2.1, 2.9	4.8, 2.4
	P ³ (L, W)	P ⁴ (L, W)	M ¹ (L, W)	M ² (L, W)	M ³ (L, W)
High	3.1, 3.7	3.9, 5.1	4.4, 5.2	5.0, 6.7	4.0, 5.2
Low	— —	— —	4.1, 5.0	4.5, 5.5	3.5, 4.8
<i>n</i>	1	1	3	6	7
Mean	— —	— —	4.2, 5.1	4.7, 6.2	3.8, 5.1
SD	— —	— —	0.12, 0.09	0.16, 0.40	0.15, 0.13
CV	— —	— —	2.9, 1.8	3.4, 6.5	3.9, 2.5

vicinity of the type section northeast of the town of Lost Cabin, and are both geographically and geologically restricted. Certainly the fauna from the Lysite Member alone cannot be said to represent all time elapsed between the Graybullian and the Lostcabinian. No taxon of *Hyopsodus* is restricted to the Lysite Member, although an abundance of *H. powellianus-powellianus* marks Lysitean strata in the Wind River and Bighorn basins.

The type of “*Hyopsodus browni*” (ACM 3232) is a smaller specimen of the *Hyopsodus powellianus* lineage rather than being referable to *H. sp.*, cf. *H. mentalis*, based on its posteriorly extended hypocone on M³, long anteroposterior length of P³, and the degree of development of the hypocristid on P₄. Other specimens, such as CM 19834, are similar to ACM 3232 in size and also conform more closely to the diagnosis of *H. powellianus-powellianus*. If the Lysite Member sample, referred here to *H. powellianus*, does represent a mixture of *H. powellianus-powellianus* and *H. sp.*, cf. *H. mentalis* (Kelley and Wood, 1954, and Guthrie, 1967, also support the presence of only one large Lysitean lineage of *Hyopsodus*), then there is considerable overlap between them in size and virtually complete overlap in morphology. Considering the morphology of *Hyopsodus sp.*, cf. *mentalis* as it appears in the San Juan Basin and at the non-Lysite Member localities in the Wind River Basin, this appears to be an unlikely possibility. No specimens of undoubted *H. sp.*, cf. *H. mentalis* morphology were identified in the CM or ACM collections from the Lysite Member. Larger specimens of *Hyopsodus* from the ?early Lysitean Cole localities (CM localities 1903 and 1904), approximately 60 km to the southeast (see Fig. 23, Table 2) in the Casper Arch area, correspond to the diagnosis of *Hyopsodus sp.*, cf. *H. mentalis* and are referred to this taxon here.

Specimens from the ?Lysitean/?Lostcabinian Okie Trail and Pavillion localities (see larger specimens on histograms in Fig. 22) are nearly identical to *H. sp.*, cf. *H. mentalis* as it is known in the San Juan Basin—significantly smaller and different in P₄ morphology than Lysitean specimens of *Hyopsodus powellianus-powellianus*. The referred lower dentitions are especially like *H. sp.*, cf. *H. mentalis* in featuring a very large entoconid on P₄ and in lacking the more inflated talonid cusps typical of *Hyopsodus powellianus*. The size and morphology of this material are outside the range of any lineage segments of *Hyopsodus paulus*, and

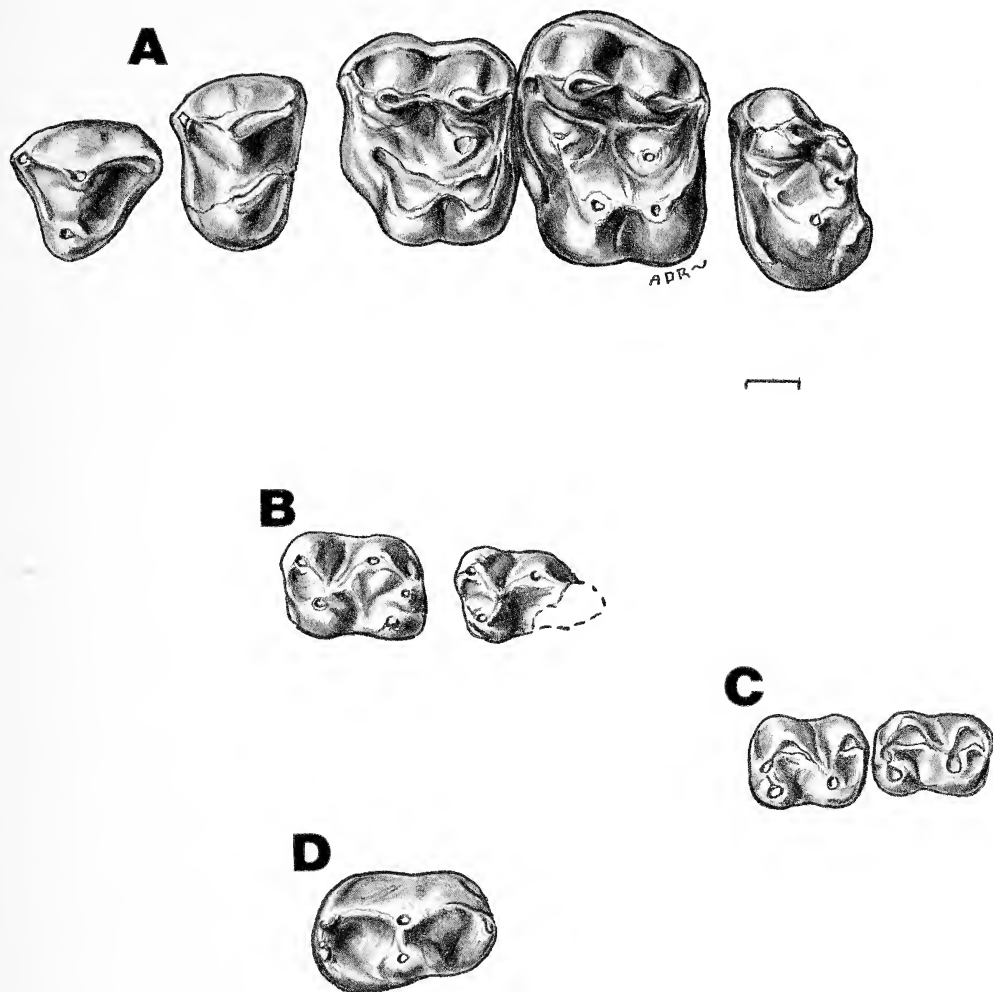


Fig. 23.—Specimens of *Hyopsodus* from localities other than the Lysite and Lost Cabin members of the Wind River Formation. A, CM 4915 (early *H. powellianus*) from the Piceance Basin; B, CM 10472 (*H. minor*) from the Piceance Basin; C, CM 445976 (?*H. minor*) from the San Juan Basin; D, CM 45996 (*H. sp.*, cf. *H. mentalis*) from the ?early Lysitean Cole locality. Scale equals 1 mm.

similar *Hyopsodus* does not occur at any of the much better sampled, undoubted Lostcabinian localities in the Wind River Basin. The sample size from the Okie Trail and Pavillion localities is small (a total of 26 catalogued specimens) but this material may indicate a limited immigration from another source area, followed by a local extinction. At this point, this conclusion should be regarded as purely speculative. The biostratigraphic record of *Hyopsodus* sp., cf. *H. mentalis* or specimens similar to it terminates with these localities. It may be noted that Gingerich (1976a) reports two specimens from early Lostcabinian sediments of the Willwood Formation whose lower first molars cluster around a mean \log_{10} of 1.25. They are attributed to a new *Hyopsodus* lineage trend but appear to be anomalous on the graph presented. *Hyopsodus* sp., cf. *H. mentalis* possesses molars that

exactly correspond to Gingerich's anomalous specimens. The immigration of a distinct taxon is a better explanation for these and similar *Hyopsodus*.

Alternatively, the lower molar size distribution of *Hyopsodus* at the Wind River Okie Trail area could be interpreted as representative of an earliest Bridgerian time—representing a mix of *Hyopsodus paulus-paulus* and *Hyopsodus minusculus* (see discussion of small specimens under *H. minor*). For the present time, however, the P_4 morphology of specimens that preserve this tooth seems consistently derived with respect to the *Hyopsodus paulus* lineage and much more like that of San Juan Basin *Hyopsodus* of similar size. Five uncatalogued specimens containing P_4 collected since 1989 are virtually identical. Also, the representation of the large (intermediate) and small forms of *Hyopsodus* at Okie Trail is numerically biased in favor of specimens referred here to *H. sp.*, cf. *H. mentalis*—different from Gardnerbuttean localities where *H. paulus* and *H. minusculus* occur with approximately equal frequency. Stratigraphic relations (Stucky et al., 1990) and the presence of *Lambdotherium* also suggest that the Okie Trail localities are early Lostcabinian rather than Gardnerbuttean.

KEY TO IDENTIFYING THE TAXA OF EARLY EOCENE *HYOPSODUS*

The following summary of change in *Hyopsodus* species-lineage taxa may be useful in discriminating *Hyopsodus* specimens from the Wasatchian and Bridgerian of North America.

Hyopsodus paulus is intermediate in size (see Tables 3, 4) and is detectably larger than *H. loomisi* at localities with a good sample size. In Graybullian *Hyopsodus paulus*, the lower third molars are short, generally equal to or shorter than the second molars. Lower premolars are long, but transversely wide (rather oval in occlusal view), bunodont with the trigonid cusps dominating the teeth. The paraconid is frequently large on the low-crowned lower molars. Upper molar hypocones and external cingula are not well formed but are stronger than those of *H. loomisi*. Lysitean *Hyopsodus paulus* retains relatively long lower fourth premolars, but has more defined protoconids and metaconids and more basined and proportionately longer talonids. M_3 is equal to or longer than M_2 . Lower molar paraconids occur less frequently and are smaller; hypocristid and metacristid are stronger. Upper molars have distinct labial cingula and may show external ribs on exterior margins of the paracone and metacone. By the earliest Bridgerian, *Hyopsodus paulus* is somewhat larger in molar size and more derived on average in the degree of expression of characters mentioned above as well as shortening of the lower premolar series, anterior shifting of the molar protoconid and apex of hypoconid, lingual placement of the hypoconulid, labiolingual compression of upper molar and premolar paracone and metacone, and increased lophodonty of all cusps and the connecting crests between them. West (1979a) cites more strongly connected upper molar protocones and hypocones in Bridgerian *H. paulus*, however, analysis of the entire *H. paulus* lineage sequence suggests that this is an artifact of the development of wear facets, and can also be observed in Graybullian specimens. *Hyopsodus loomisi* more frequently shows a distinct valley between these cusps. *Hyopsodus paulus* is easily distinguished from significantly smaller lithosympatric *H. minor* and *H. minusculus*.

Hyopsodus powellianus enlarges in size through time and increases swelling of the cusps, prominence of the molar entostylid and P_4 posthypocristid, broadening of the upper premolar and molar anterior cingula as well as the hypocrista of M^3 .

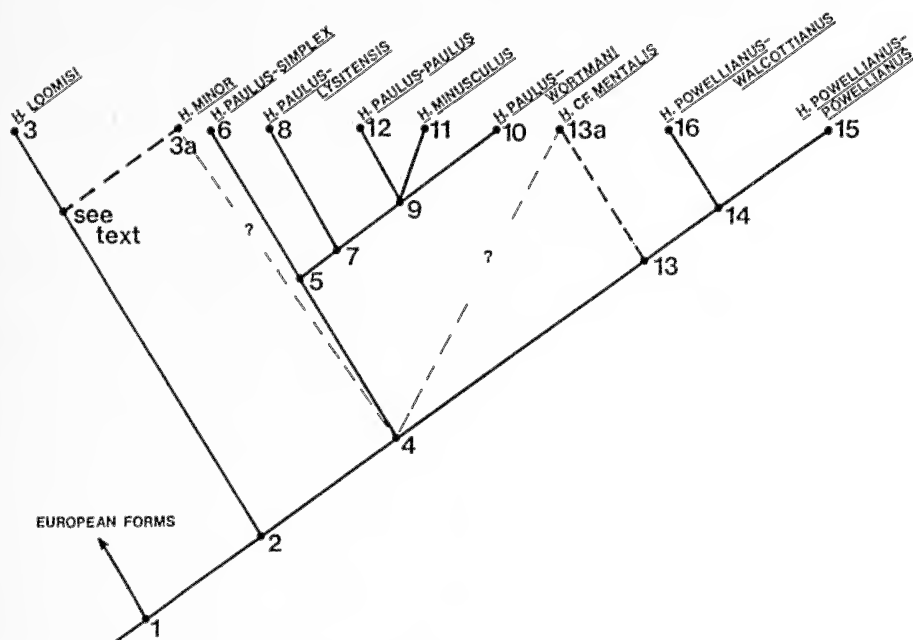


Fig. 24.—Proposed cladistic relationships of Wasatchian and early Bridgerian *Hyopsodus*. Characters discussed in text.

The compression of cusps noted in *Hyopsodus paulus* is not apparent in this lineage but, in parallel, it does show increase in relative size of upper and lower third molars, reduction of molar paraconids (usually to an even greater degree than lithosympatric specimens of *H. paulus*), and in the slight development of labial ribs on the upper dentition. Of course, as *H. powellianus* is the largest-sized taxon of *Hyopsodus*, it is easily discriminated at localities with a fair sample of *Hyopsodus*.

At the level of resolution undertaken in this revision, the phylogenetic pattern of *Hyopsodus* is one of gradually evolving morphologic lineages. One intermediate-sized lineage (*Hyopsodus paulus*) occurs throughout the Wasatchian and Bridgerian, and three smaller forms are related to this lineage at different evolutionary stages (*Hyopsodus loomisi*, *Hyopsodus minor*, and *Hyopsodus minusculus*), as are the large taxa *Hyopsodus powellianus* and *Hyopsodus* sp., cf. *H. mentalis*.

RELATIONSHIPS

If the diagnoses of all of the taxa of *Hyopsodus* are considered to be descriptions of discrete, nonchanging entities, then it is possible to construct a cladogram of the known Wasatchian and early Bridgerian taxa. Problems may arise because the dental characters are "average" morphologies and, in the case of lineage segments, parts of continua. Figure 24 is an illustration of the proposed cladistic relationships. Some nodes partly reflect more frequently expressed or more highly developed characters as opposed to a character's absolute presence or absence. The cladogram was constructed in order to discuss derived features at the numbered nodes as traits of morphologic discrimination. However, as mentioned ear-

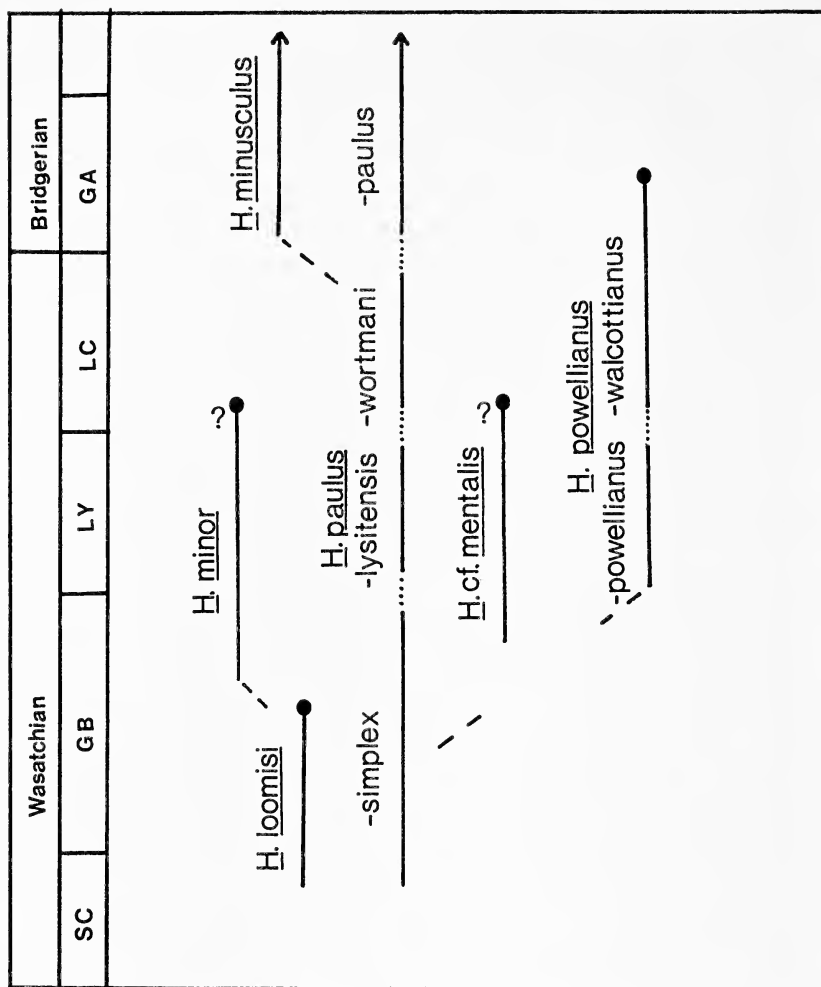


Fig. 25.—Proposed phylogenetic relationships of species and species lineages of Wasatchian and early Bridgerian *Hyopsodus*. Abbreviations; SC, Sandcouleean; GB, Graybullian; LY, Lysitean; LC, Lostcabinian; GA, Gardnerbuttean.

lier, this cladogram obscures evolutionary information inferred from the combination of a large number of specimens and sufficiently precise stratigraphic data. Therefore, a nondichotomous phylogenetic classification is also given (Fig. 25). The lineage-segment etymology used in this study expresses evolutionary and relationship statements in its informal trinomials as well. Due solely to cladistic convention, Figure 24 is a more complicated explanation of *evolutionary pattern* in *Hyopsodus* than is necessary.

Computer algorithms were not used to generate this tree. Many dilemmas were faced during the course of systematic work with *Hyopsodus*. The rooting of this tree was not a problem; *Hyopsodus* as a genus was not assessed for relationship to other generic-level taxa; therefore, what was considered primitive for a *Hyopsodus* taxon was based on relative time of occurrence of the character or its

frequency. The variability of characters made them impossible to score either as present or absent or objectively on a "one-to-three" (for example) range. The initial weighing of character frequencies based on stratigraphic information would consequently weigh the ensuing cladogram.

Cladogram Node 1 describes the derived dental features of *Hyopsodus*. Arc-toeyonid condylarths and *Haplomylus* were used as outgroups. Derived features are: two primary cones on P^4 ; hypocone large and approaching height of protocone on M^{1-2} (much larger than any "pericone" on anterior cingula); distinct hypocone or hypocrista on M^3 ; lower molar hypoconulids enlarged and comparatively posterolingually oriented; M_3 hypoconulid relatively large, crescentic, and separated from hypoconid and entoconid; P_4 simple in cusp morphology, no ectoflexid or anteriorly placed paraconid; paraconid not structurally distinct on M_1 (if present, it appears as a cuspule on the preprotocristid). Some characters, such as P_{3-4} morphology and small, unspecialized anterior dentitions appear to be decidedly primitive for Eutheria as a whole. However, the retention and modifications of this morphology in *Hyopsodus*, as compared to many arctocyoniids, meniscotheriids, phenacodontids, and other known faunal contemporaries, are unique among Eocene mammals of comparable or larger body size. The European forms of *Hyopsodus*, which are still incompletely known, seem to share the above described characters. Since they appear to be quite primitive they are portrayed in Figure 24, but were not cladistically resolved in this study. Very primitive fossils from the People's Republic of China will be described soon (M. R. Dawson and K. C. Beard, personal communication), but were also not included.

Node 2 lists the shared/derived characters of *Hyopsodus loomisi* and all other *Hyopsodus* from the North American early to middle Graybullian record. These are: very small upper and lower third molars; only partly distinct hypoconulid on M_3 ; low crowned, conical cusps on all teeth; very high frequency of vestigial paraconid on M_1 , high frequency on M_2 and M_3 ; molar cingula relatively weak; P_{3-4} long and wide with large-based, amorphous protoconid (not distinctly differentiated from other trigonid cusps).

Unique characters of *Hyopsodus loomisi* (Node 3) are: small size; very low-crowned dentitions with poorly developed connecting lophs between cusps; transverse width of M^1 frequently close to width of P^4 ; anterior and external cingula severely reduced or absent on upper dentition; M^3 hypocone very restricted or absent, hypocrista weak, metacone not distinct; M^{1-2} hypocone small, somewhat labially situated and distant from protocone; lower molar entoconid small and labial; M_{1-2} trigonid width usually greater than talonid width.

Node 4 indicates shared/derived characters of all other forms of *Hyopsodus*, spanning the Graybullian to the Gardnerbuttean, exclusive of *Hyopsodus minor* (dental characters indicated by Node 3a below). These are: P^4 most frequently narrower than M^1 ; M^3 hypocone and metacone more highly developed, M^3 appears "somewhat bent" on posterior margin; more strongly developed protoloph on M^{1-3} , anterior and external cingula well defined; M^{1-2} hypocone strong, relatively lingual, and more nearly equal in height and size to protocone; P_4 paraconid more distinct; M_{1-2} with stronger and more lingually placed entoconid, transverse width of talonid usually greater than width of trigonid.

All members of the *Hyopsodus paulus* lineage are united by the shared or secondarily modified characters at Node 5. The most important and relatively static character here is intermediate size. Other characters dissimilar from the *Hyopsodus powellianus* lineage (Nodes 13–16, below) are: distinct but not ex-

panded anterior cingula on the upper dentition posterior to P^2 ; M^3 metacone more labial, hypocone usually present but not part of posterior hypocrista flange; entostylid of lower molars, when present, is small and not inflated at base; molar metaconid less tall, protoconid not as anteriorly placed.

The Lysitean species *Hyopsodus minor* is represented at Node 3a. Some characters indicate it is most closely allied to *H. loomisi*; however, if this is a direct ancestor-descendant relationship, the "*H. loomisi*–*H. minor* lineage" also appears to have paralleled *H. paulus* in some aspects of anagenetic change. Although *Hyopsodus minor* shares small size, transversely compressed lower molar talonids, and weak hypocones on M^{1-2} with *Hyopsodus loomisi*, it also features proportionately larger upper and lower third molars, moderately developed cingula, shorter fourth lower premolars with an entoconid, and somewhat larger M^1 . These features are, in turn, shared with Graybullian and Lysitean segments of the *Hyopsodus paulus* lineage. Unfortunately, the upper dentition of *H. minor* is not well known in the Wind River collections, and its diagnosis is based on limited material. A greater number of *Hyopsodus loomisi* upper dentitions were examined in this study. Upper molars of *Hyopsodus minor* appear more transversely compressed or "fat" than most other *Hyopsodus*, but not as square in occlusal view or with as continuous cingula as *Hyopsodus minusculus*. Some specimens have weak ribs on the external margins of the paracone and metacone as in *H. paulus*.

Node 6 defines the morphology of lineage segment *Hyopsodus paulus*–*simplex*, if this taxon is treated as a static entity, rather than an informal, most primitive stage of *Hyopsodus paulus*. Characters at this node are the same as those listed at Node 5, expressed to the degree indicated by the lineage-segment diagnosis in practically all specimens.

Node 7 represents the informal boundary point of frequently expressed derived features separating specimens of *Hyopsodus paulus*–*lysitensis* from the temporally preceding *H. paulus*–*simplex*. As with the Nodes 5 and 6 combination, Node 8 merely marks the presence of the character states of Node 7 in the vast majority of specimens. Node 7 indicates: slight transverse compression of upper premolar paracone and upper molar paracone and metacone; M^3 nearly as labiolingually wide as M^1 ; external ribs expressed more frequently; entoconid more nearly separate from hypoconulid on all molars, particularly M_3 ; P_4 shorter, protoconid more distinctly separate from other trigonid cusps, entoconid common on posthypocristid; P_{3-4} with relatively longer talonids (as compared to general trigonid length); lower molar paraconid and entostylid less common.

At Node 9 are the more advanced characters shared by the Lostcabinian and Gardnerbuttean small and intermediate lineages of *Hyopsodus*. These are: transversely compressed paracones and metacones on upper cheek teeth with strong labial ribs; M^3 metacone well developed and labially situated; anterolabial wings of protocone on P^{3-4} and loph between upper molar protocone and paraconule stronger; shorter lower premolar series; infrequent occurrence of paracone on M_1 , very infrequent paracone on M_2 ; hypoconulid lobe of M_3 well developed and more nearly separate from entoconid and hypoconid on majority of specimens; generally more lophodont (crests more distinct, cusps less so) dentition. These characters also describe *H. paulus*–*wortmani* (Node 10), which is morphologically "intermediate" between and temporally precedes both of the Bridgerian forms, *H. paulus*–*paulus* and *H. minusculus*. No autapomorphies distinguish *H. paulus*–*wortmani*. Node 9 is at a trichotomy rather than as a sister group to *H. minusculus*.

or *H. paulus-paulus* because it is impossible to determine which of the latter taxa share more in common with *H. paulus-wortmani*.

Hyopsodus paulus-paulus and *H. minusculus* (Nodes 12 and 11) share the characters of *H. paulus-wortmani* (Nodes 9 and 10) in common, but differ in the following ways. *Hyopsodus minusculus* (Node 11) is derived in the high frequency of occurrence of: small size; shortened P_4 with anteriorly inflected paraconid and elevated labial margins of hypocristid with no entoconid (tooth appears notched); more elongate lower molars with hypoconulid often separated from entoconid by a notch; molar cristid obliqua meets trigonid somewhat more labially; upper molars not as wide (more nearly square than) as in *H. paulus-paulus*, paraconule small and not crescentic; hypocingula of M^3 not as posteriorly expanded, more closely follows posterolingual base of protocone.

Hyopsodus paulus-paulus (Node 12) is distinguished by: uniformly larger than *H. minusculus* (average size also larger than *H. paulus-wortmani*); lingual shifting of M_1 and M_2 hypoconulid; entoconid more anterolingually distant from hypoconulid and often connected by strong crest; more anteriorly placed molar protoconids and generally more lophodont crests; P_4 shorter than in *H. paulus-wortmani*; P_4 more distinctly basined (not severely notched) with entoconid more common than in *H. minusculus*; P_4 metaconid more distinct; wider upper molars (especially M^2) than in *H. minusculus*, more distinct and crescentic paraconules; more extensive hypocrista on M^3 .

Node 13 describes the derived characters of large Wasatchian and early Bridgerian *Hyopsodus*. These are: large size, anteriorly expanded cingula on upper dentition, larger parastyle on P^{3-4} , M^3 metacone strong but somewhat more lingual in comparison to paracone, long P_4 with well-defined talonid, relatively large M_{1-2} hypoconulid. This diagnosis also defines specimens of *Hyopsodus* sp., cf. *H. mentalis* (Node 13a), which is close to the *Hyopsodus paulus* lineage at the Lysitean stage but is significantly larger and usually features a very strong entoconid on the posterolingual margin of the P_4 posthypocristid. In the latter character, *H. sp.*, cf. *H. mentalis* is most similar to lineage segment *H. paulus-simplex* or *H. paulus-lysitensis*, whereas molar size is closer to the *Hyopsodus powellianus* lineage.

Node 14 represents shared/derived characters of the *Hyopsodus powellianus* lineage. At this node are: very large size, P^3 triangular in occlusal view, bases of protocone and hypocone on M^{1-2} swollen, hypocrista and hypocone of M^3 posteriorly splayed (amplification of "bent" character discussed at Node 4), lower molar entostylid and metastylid very common and large, posthypocristid on P_{3-4} strong (entoconid variably present on P_4) and often partially encloses talonid, hypoconulid lobe of M_3 very large.

The differences between lineage segments *H. powellianus-powellianus* and *H. powellianus-walcottianus* are shown above Node 14. Node 15, the character states of *H. powellianus-powellianus*, indicates: lower molar metaconid large and tall, paraconid absent or very reduced on M_{2-3} (less frequently present or as large as in the *Hyopsodus paulus* lineage); entostylid and entoconid variably large and aligned with hypoconulid on lower molars. Otherwise, all *H. powellianus-powellianus* specimens conform to the diagnostic characters of Node 14, at least those from the Lysitean of the Wind River and Bighorn basins.

Hyopsodus powellianus-walcottianus (Node 16) is distinct in its extremely large size; very large entostylids on lower molars; molar protoconids anteriorly

oriented; very rectangular P_4 with strongest posthypocristid of all *Hyopsodus*; and possibly, larger hypocone on hypocrista of M^3 .

As has already been discussed, some of the best defined "monophyletic" taxa represented in this cladogram are the relatively poorly known ones—those with either a limited record or those from single temporal intervals. For example, specimens of *Hyopsodus minor* are underrepresented in the Eocene record except in the Lysite Member of the Wind River Formation, where they appear quite distinct from other lithosympatric *Hyopsodus*. The same is true of *Hyopsodus powellianus-walcottianus*. Both taxa, distinct at single biostratigraphic levels, show overlap with specimens from preceding intervals—the former with Piceance Basin *H. minor*, the latter with specimens of *H. powellianus-powellianus*. Given the evidence for considerable anagenesis between successive specimens of *H. paulus*, it is apparent that what are designated here as taxonomically "stable" forms do change through time and that expressing this change in a cladogram may distort what can be inferred of paleobiologic reality.

The "species" *Hyopsodus paulus* is paraphyletic; *Hyopsodus powellianus* would be also, if *H. powellianus-powellianus* is the sister taxon of *H. sp.*, cf. *mentalis*. The cladogram depicts *Hyopsodus paulus-paulus* as the sister taxon of *H. minusculus*, with each preceding lineage segment of *Hyopsodus paulus* being successively more primitive. *Hyopsodus paulus-lysitensis* and *H. paulus-simplex* are united with *Hyopsodus paulus-paulus* only on the basis of primitive characters. If the species is the operational unit of a cladogram, then the lineage-segment taxa are noncladistic. This is an example of how species-lineage segments are difficult to resolve cladistically because, by definition, they have arbitrary boundaries based on the combination of frequency of character expression and overlain stratigraphic data. The species *Hyopsodus paulus* is paraphyletic. Paraphyly is, without question, a cladistic sin, but does not trespass on the description of biologic change through time. Lineage segments go further; they attempt to describe change over time. Recognizing these conflicts, it is worthwhile to review and summarize the overall pattern of *Hyopsodus* evolution (Fig. 25). The conclusions of this study reflect the choice of simplifying *Hyopsodus* taxonomy by allying specimens of similar, but not exactly the same, morphology over the option of resurrecting the numerous geographic and temporal species of past workers. This reflects a philosophy regarding paleontological "species" and an attempt to discern a pattern of morphologic change and overlap as taxa proceed through time.

One fact concerning the diversity of Wasatchian and early Bridgerian *Hyopsodus* is true for all localities. **Never** are more than three species of *Hyopsodus* found in lithosympatric association. Generally, these taxa can be classified as small, intermediate, and large in size. Two fundamental considerations argue against concluding that this is an indication of evolutionary stasis within early Eocene *Hyopsodus* taxa. First, each species lineage (lineage, not segment), defined on derived features at the point of its first observable dental distinction, undergoes considerable anagenetic change through time. For example, *Hyopsodus paulus-paulus* is very distinct from *H. paulus-simplex*. *Hyopsodus paulus-simplex* as a discrete taxon (ignoring subsequent lineage segments of *H. paulus*) is morphologically much closer to *Hyopsodus loomisi* owing to the more frequent occurrence of primitive characters such as small third molars and molar paraconids. Were it not for other key character differences that are later canalized and far more strongly expressed (anagenesis), *H. paulus-simplex* and *H. loomisi* could not be as readily distinguished. *Hyopsodus paulus-paulus* represents a form which

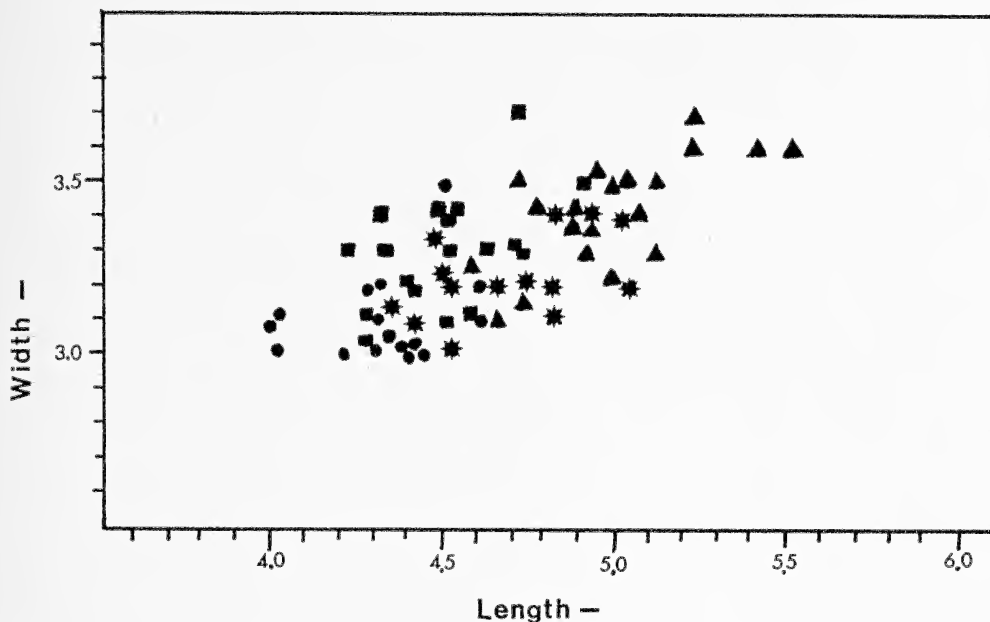


Fig. 26.—Length/width plot of *Hyopsodus paulus* lower third molars from selected localities. Horizontal and vertical axis are in mm. Symbols: circles, Graybullian, Dorsey Creek; squares, Lysitean, Davis Draw; starbursts, Lostcabinian, "K-6, B-2 horizon"; triangles, Gardnerbuttean, CM loc. 34 (20 randomly selected specimens).

more strongly and more frequently emphasizes characters first appearing in *H. paulus-simplex*, such as large molar hypocones, well-distinguished cingula, and wide lower molar talonids. Anagenetic increase in the comparative size of the lower third molar of *Hyopsodus paulus* is portrayed in Figure 26. The relative size of M^3 parallels this development. Like the *Hyopsodus paulus* lineage, *Hyopsodus powellianus-walcottianus* is larger and emphasizes derived dental morphology found in its Lysitean ancestors.

Another argument against stasis in early Eocene *Hyopsodus* is the evidence that taxa of similar size (*H. minor*, *H. minusculus*) evolved iteratively in the Wasatchian and early Bridgerian. This pattern was strongly indicated by Gingerich (1974a), based on the change in size of M_1 through time in the Bighorn Basin (Fig. 27), and is more generally corroborated by dental characters in this study. What this evolutionary pattern implies remains uncertain; Gingerich (1974a) failed to remark on the systematic implications or geographic extrapolation of *Hyopsodus* evolution outside of a single basin. As yet, the role of immigration of closely related forms has still not been discussed. Resolving these problems (with any fossil taxon) remains a problem for future paleontological research. Less formal examination of *Hyopsodus* from Bridgerian and Uintan localities suggests that West's (1979a, 1979b) declaration of stasis as the rule for later Eocene lineages can no longer be accepted or cited as valid. Only size is relatively constant in the Bridgerian. Preliminary, unpublished research does indicate morphologic change during this interval.

The small forms *Hyopsodus minor* and *Hyopsodus minusculus* are not closely related (based on a lack of shared/derived attributes other than size) and are

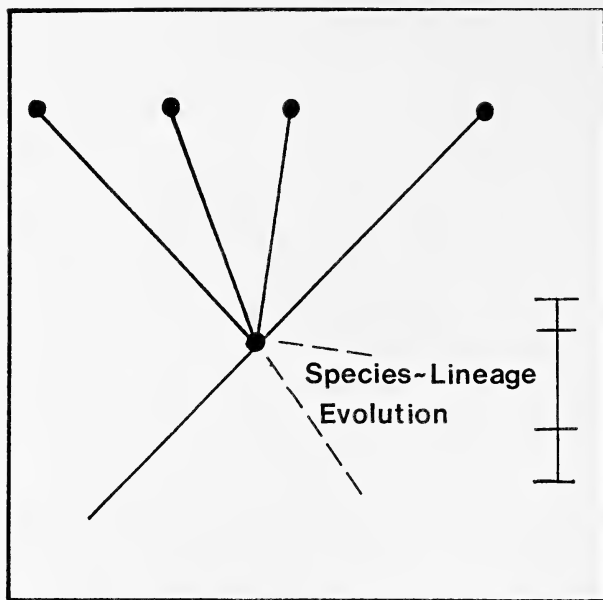


Fig. 27.—Pattern of *Hyopsodus* evolution in the Willwood Formation, as determined from \log_{10} of length \times width of first lower molar. From Gingerich, 1974a.

temporally disjunct. Wind River *H. minor* appears to be close to *Hyopsodus loomisi* in certain key characters (see above) and is very similar to the slightly larger specimens from the San Juan and Piceance basins. *Hyopsodus minusculus*, on the other hand, possesses many advanced characters in common with *Hyopsodus paulus-paulus* and, other than being smaller in average size, closely corresponds in morphology to some specimens of Lostcabinian *Hyopsodus paulus-wortmani*. Therefore, it seems that two small lineages of *Hyopsodus* evolved independently during the early Eocene and that the synonymy of *Hyopsodus minor* and *H. minusculus* (= "*H. wortmani*" of previous studies; Gazin, 1968) is not correct. At least within the Wind River Basin, this appears to be an example of iterative evolution of similar size types within the same genus. As another example, in the late Eocene, *Hyopsodus uintensis* (Osborn, 1902) and *Hyopsodus sholemi* (Krishalka, 1979) became almost as large as Wasatchian *Hyopsodus powellianus*, but there is no evidence the former are related to the latter. Large-sized *Hyopsodus* is completely absent from the intervening and densely sampled Bridgerian localities of the Rocky Mountain Interior (Gazin, 1968; West 1979a, 1979b). In the early to middle Wasatchian, *Hyopsodus* sp., cf. *H. mentalis*, possibly the result of an iterative southern radiation, may also have occupied a large *Hyopsodus* niche, particularly in the basins south of Wyoming.

Hyopsodus paulus is abundantly known from earliest through latest Wasatchian localities; although it undergoes directional change in dental morphology, it shows little increase in molar size in this interval. Members of this lineage are probably ancestral to *Hyopsodus powellianus*, *Hyopsodus minusculus*, and possibly *H. sp.*, cf. *H. mentalis* at different times in its Wasatchian history. Relationship with *Hyopsodus powellianus* is supported by shared/derived characters, whereas the gradual divergence of *H. minusculus* can be more directly inferred from litholog-

ically successive populations of *Hyopsodus* from the late Lostcabinian and Gardnerbuttean of the Wind River Formation. A similar gradual divergence has been noted in *Leptomeryx* from the Chadronian Flagstaff Rim area of Wyoming (Heaton, 1989), although in this study of *Hyopsodus*, no judgments are made concerning sympatric speciation. Again, although *Hyopsodus paulus* may indeed comprise many closely related biological species and subspecies, as a group, all the specimens share morphology not expressed with a similar frequency in other *Hyopsodus* taxa. The reasons *Hyopsodus paulus* is recognized as a single species lineage for specimens from the earliest to middle Eocene (see Table 1, the type is Blackforkian) are twofold: (1) an intermediate-sized lineage of *Hyopsodus* (i.e., *H. paulus*) can be differentiated comparatively at practically all localities within this long interval. The examination of intermediate-sized specimens suggests a morphologic continuum (anagenetic rather than cladogenetic) when arranged in bio- or lithostratigraphic order. Although possible speciation events in this lineage cannot be abstractly rejected as possibilities, there is no positive evidence to support them; and (2) naming geographic or stratigraphic species would expand the species diversity of the genus without any proof of cladogenesis (see Krishalka and Stucky, 1985). Subspecies seem inappropriate for the fossil record given that workers rarely agree on species definitions and because they were never meant to denote temporally successive taxa.

Specimens of *Hyopsodus paulus* from the Lostcabinian (*H. paulus-wortmani*) may represent two biological species (one being incipient *H. minusculus*) from this time period, at least in the Wind River Basin. However, the overlap of characters and the normal size distribution from single localities cannot be systematically unravelled. These characters are associated with intermediate and small-sized populations of *Hyopsodus* (*H. paulus-paulus* and *H. minusculus*) in the earliest Bridgerian. This "mixed" assessment of *H. paulus-wortmani* dental morphology could not have been identified without knowledge of the morphological distribution of temporally succeeding Bridgerian specimens of *H. paulus-paulus* and *H. minusculus*.

Apparently, *Hyopsodus minusculus* continued to average smaller in molar size throughout the Blackforkian. *Hyopsodus minusculus* M₂ length averages 3.28 mm at Church Buttes (low Bridger B, USNM collections) according to West (1979a: 32), smaller than at CM loc. 34 (Gardnerbuttean), and similar in size to Lysitean *H. minor*.

STRATIGRAPHIC AND GEOGRAPHIC OCCURRENCE

The abundance of *Hyopsodus* has been cited as a drawback for complete systematic review. Systematics aside, data concerning the frequency of occurrence of taxa of *Hyopsodus* at localities may bear on interpretations of their paleoecology and distribution. These matters are considered in this section.

The total number of *Hyopsodus* specimens collected from the Wind River Basin, tallied from the CM specimen catalogue, are listed in Table 11. These numbers are approximate and may be low estimates, particularly for *Hyopsodus powellianus-powellianus*, *Hyopsodus paulus-paulus*, *Hyopsodus paulus-lysitensis*, and *Hyopsodus minusculus*, because many older CM catalogue numbers may refer to batches of five to 50 isolated jaws and teeth, some of which can be fragmentary or represent two or more taxa. The totals are qualitatively (proportionately) fairly accurate even though the absolute number of specimens is much higher.

Table 11.—Approximate number of CM specimens of *Hyopsodus* taxa tallied by catalogue number counts. Specimens counted are from the Lost Cabin and Lysite members of the Wind River Formation.

Taxa	Approximate number of CM specimens
Gardnerbuttean	
<i>H. paulus-paulus</i>	320
<i>H. minusculus</i>	260
<i>H. powellianus-walcottianus</i>	1
Lostcabinian	
<i>H. paulus-wortmani</i>	160
<i>H. powellianus-walcottianus</i>	11
Lysitean	
<i>H. paulus-lysitensis</i>	310
<i>H. powellianus-powellianus</i>	440
<i>H. minor</i>	35

In the Gardnerbuttean of the Wind River Formation, the intermediate-sized *Hyopsodus paulus-paulus* and the small *Hyopsodus minusculus* occur in relatively equal numbers, comprising 55 and 45 percent of total specimens, respectively. Twenty field seasons of prospecting in the Gardnerbuttean have only recently yielded one specimen of *H. powellianus-walcottianus*, from less intensively examined upper grey beds at CM loc. 34. Stratigraphically lower, in the Lostcabinian of the Lost Cabin Member, *Hyopsodus paulus-wortmani* outnumbers the much larger *H. powellianus-walcottianus* 94 percent to six percent. More recent collecting has added about 100 catalogued and uncatalogued dentitions of *H. paulus-wortmani*.

The *Hyopsodus* size distribution in the Lysite Member of the Wind River Formation contrasts markedly with that of the Gardnerbuttean and Lostcabinian of the Lost Cabin Member. Here again, the intermediate-sized *Hyopsodus paulus (lysitensis)* is well represented by 40 percent of total specimens. However, the large form, *H. powellianus-powellianus* is even more common at 56 percent of total *Hyopsodus*. The small *H. minor* (four percent of total) is not common—and four percent may be a high estimate because many specimens of this species were separated from their original CM “batch” number and recatalogued under individual numbers during the course of this study to increase sample size.

The possibility that these differences in specimen abundance are due to collecting biases is fairly remote. Although the Lysite Member as a whole is generally somewhat more coarse-grained than the Lost Cabin Member, both the collecting procedures and the size of fossil elements found are the same. *Hyopsodus minor* specimens are no more difficult to find when surface prospecting than those of small primates, carnivores, and insectivores that are commonly recovered. *Hyopsodus minusculus*, similar in size to *H. minor*, is as frequently collected from Bridgerian localities as is the larger *H. paulus*. It does not appear likely that sorting or accumulation differences among mudstone horizons are responsible for the frequency of occurrence of *Hyopsodus* taxa in surface finds.

As a contrast to surface prospecting tallies, at the Lostcabinian CM Buck Spring Quarries, the relative abundance of *Hyopsodus* (see Stucky et al., 1990; data through 1988) is only five of 369 mammal specimens, versus 18 of 82 total specimens obtained by prospecting this area. The quarry sample is dominated by

very small taxa and represents differential preservation (see Stucky et al., 1990) from the surrounding floodplain mudstones.

Outside of the Wind River Basin, the representation of *Hyopsodus minor* in the DeBeque Formation of Colorado is much better (Kihm, personal communication, 1989). Most well-preserved upper dentitions examined from the CM collections are from the Piceance Basin. If *Hyopsodus* as a whole is preferentially preserved because it was very common, as indicated by the data of Stucky et al. (1990), then probably, like *Meniscotherium* in the Lostcabinian (Gazin, 1965), *H. minor* was never common in the Wind River Basin. A similar phenomenon may explain the paucity of *Hyopsodus powellianus-walcottianus* specimens in the Lostcabinian. Gazin (1965) suggested that large *Hyopsodus* and *Meniscotherium* were incompatible, although neither taxon is common in the Lostcabinian of the Wind River. Other possibilities might be that taxa of *Hyopsodus* were environmentally specific or subject to broader competitive exclusion than that implied by competition with a single taxon (in this case, *Meniscotherium*).

Considering the factors discussed above, the following conclusions are offered as explanations for the pattern and frequency distribution of *Hyopsodus* in the Wind River Basin: (1) *Hyopsodus minor* was uncommon (less so than in the Bighorn and southern basins) and is restricted to the Lysite Member and CM localities 936 and 1903. It is possible that *H. minor* may have favored a paleoenvironment different from that of the Wind River Basin margins in the early Eocene, or, alternatively, was becoming rare by the time of Lysite Member deposition. This cannot be tested because aside from the Lysite Member, Lysitean time is very sparsely represented in the basin; (2) the large form, *H. powellianus-powellianus* is very common in sediments of the Lysite Member and may have been better adapted to this environment. This abundance of a large species may conflict with Gingerich's (1989) findings of smaller congeners in high-floodplain assemblages. Bown and Beard (1990) note the most frequent occurrence of large *Hyopsodus* intermediate to distal from paleochannel location as well. The Lysite Member may not fit a Bighorn Basin sedimentological model. The closely related but significantly larger *H. powellianus-walcottianus* persists from the Lostcabinian into the Gardnerbuttean in very reduced numbers, perhaps suffering in competition with other faunal elements of similar size; (3) the Gardnerbuttean horizons of the Lost Cabin Member are the first to preserve abundant numbers of small *Hyopsodus*—*H. minusculus*—which may have been well adapted to a mature river environment and associated forest canopy (as indicated by the abundance of arboreal faunal elements; see Stucky et al., 1990). The establishment of this environment in the Lostcabinian may have favored the evolution (or immigration) of *H. minusculus*. Even in the Lostcabinian, many specimens of *H. paulus-wortmani* are almost as small in tooth size as *H. minusculus*; and (4) intermediate-sized *Hyopsodus* are common at virtually all known early through middle Eocene localities in the Wind River Basin and western North America. It may have been the least habitat-restricted early Eocene *Hyopsodus*.

It is more difficult to comment with any confidence on the overall distribution of *Hyopsodus* taxa. The degree of interconnection of the western Eocene basins remains to be established. Debates on Laramide orogenic timing, degree of basin development, and classification are still in progress. Because mammalian biostratigraphy is the primary precise correlative tool for interbasinal sediments, taxa are used as indices of time. Biostratigraphy often suffers in that there is little consistency in the fossil species concept and because index taxa are often assumed

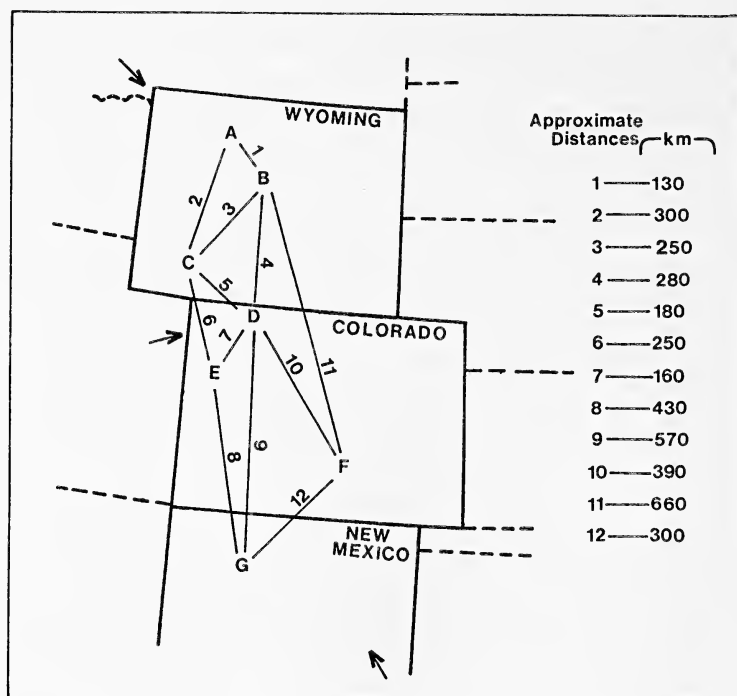


Fig. 28.—Relative distances between major western basins containing Wasatchian and early Bridgerian deposits. A, Bighorn Basin; B, Wind River Basin; C, Green River Basin complex; D, Four Mile area of "Wasatch Fm."; E, Piceance Basin; F, Huerfano Basin; G, San Juan Basin.

to be applicable as time indicators in all basins. If evolution is identified using the axis of time, and, conversely, time (biostratigraphy) needs the axis of evolution, then there is no independent data available to falsify hypotheses. If the immigration of an exotic taxon can be established, biostratigraphy is on firmer ground. However, because immigrations may depend on paleoenvironment and are not absolute time indicators, their resolution may be too coarse for anagenetic studies. These constraints can severely impact the study of vicariance and geographic distribution.

It may be possible to draw some preliminary conclusions based on the distances between Eocene basins. Absolute distances do not account for barriers or environmental differences, although their effects should not be discounted.

Of all the distances portrayed in Figure 28, that between the Bighorn and Wind River basins (Distance 1) is the least. Because the best record in each basin preserves mostly different biostratigraphic time, their respective faunas have long been strapped together to represent the Wasatchian Land Mammal Age. The characters and variation in size of *Hyopsodus powellianus* between these closest of basins in the Lysitean (based on biostratigraphy) suggest some ecological and faunal differences are present despite their relative geographic proximity. While this phenomenon may mimic modern differences between isolated basins, it may also indicate that the biostratigraphic correlation tying the Wind River and Bighorn basins is subject to the same effects. *Hyopsodus minor* may be another example of an environmentally specific taxon of *Hyopsodus*. It seems to be present

in the Lysitean of the Bighorn (Buffalo) Basin to the north (Gazin, 1968), it is fairly common in the Piceance and San Juan basins to the south, and scarce in the intervening Wind River Basin. Unless the divergence of small *Hyopsodus* occurred in all basins at the same time, this would imply a northern origin and subsequent southern migration of *Hyopsodus minor* (refer to the distances to E and G).

If *H. minor* is a real biologic entity and not merely an alliance of unrelated taxa, then the simplest explanation for its range is that it was widespread in the Graybullian/Lysitean of the Rocky Mountain Interior and its emergence may have been an intrageneric response to homogeneous community conditions in some basins, partitioning space within *Hyopsodus* as a whole. Its poor record in the Wind River Basin is a reflection of the paleoenvironment of the Lysite Member.

Unfortunately, the record from southwestern Wyoming is not stratigraphically controlled (see the plethora of *Hyopsodus* species referrals in Gazin, 1962), and the record from the Huerfano and Piceance basins do not overlap sufficiently with the better known records from other basins. This makes it difficult to assess whether the same *Hyopsodus* species were truly common to all the Wasatchian basins. The similarity in the *Hyopsodus* record in the Wind River and Huerfano basins (Lostcabinian to Gardnerbuttean) supports the hypothesis. The distance between these basins (Distance 11) is large. Dispersal between the Huerfano and Wind River basins along the eastern Laramide front was proposed by Sullivan (1986) to explain the common occurrence of the anguid lizard *Eoglyptosaurus donohoei*; this route may have also accommodated small-bodied mammals.

The large species *Hyopsodus powellianus* also seems to have been extensive in its North American distribution, except for either faunal level of the San Jose Formation. At least in the Lysitean, *H. powellianus* was smaller south of the Bighorn Basin (such as in southwestern Wyoming and in the Wind River Basin). The largest lineage segment of *Hyopsodus powellianus* (the post-Lysitean *H. powellianus-walcottianus*) possibly had its origin to the north; Bighorn Basin Lysitean specimens approach lineage segment *walcottianus* in size. Some Wind River Lysitean specimens are close to *H. powellianus-walcottianus* as well. In the Piceance Basin, Kihm's (1984) "*H. powellianus* event" seems to have marked an immigration (crossing distances 2, 3, 4, and 6) of *H. powellianus*, a species that never reached or was never common in the San Juan Basin. Yet, this species was present in the later Wasatchian of the Huerfano Basin, still north, but not geographically far from the San Juan Basin (Distance 12). The inability of the New Mexican record to "fit" with the northern record suggests that the fauna and paleoenvironment of the San Juan Basin indeed was different.

Hyopsodus paulus, on the other hand, spans the entire Wasatchian and Bridgerian, and is known even from the San Juan Basin, which otherwise features an atypical *Hyopsodus* assemblage. *Hyopsodus paulus* shows enough consistent anagenetic evolution both within and between basins to justify the conclusion that it was present everywhere and possibly was a genetically continuous biological entity through the entire early Eocene of the Rocky Mountain Interior.

In the Wind River Basin, specimens of *Hyopsodus* from the Okie Trail and possibly the Pavillion Butte area are curiously similar to *Hyopsodus* from the Almagre of the San Juan Basin. The taxa of *Hyopsodus* from these areas are not satisfactorily resolved in this study, and more detailed knowledge on the relationship of faunas from these areas might shed new light on this anomaly.

So what may be said about the validity of *H. sp.*, cf. *H. mentalis*? The diagnosis

given in this study unites all specimens assigned to this taxon. Its occurrence in the Bighorn (as "*H. lemoinianus*"), Wind River (referred CM specimens), and San Juan basins suggests it was a wide-ranging form of Wasatchian *Hyopsodus*. However, aside from the San Juan Basin, it is certainly not common, an unusual condition for *Hyopsodus* taxa. If this taxon is not arbitrary, then the most reasonable, yet cautious, conclusion would be that many specimens of *H. sp.*, cf. *H. mentalis* are representative of the *Hyopsodus paulus*–*Hyopsodus powellianus* divergence. However, this event must have occurred long before the Lostcabinian, presumably well before the time of deposition of Okie Trail and Pavillion Butte localities sediments. In the Wind River Basin, *Hyopsodus sp.*, cf. *H. mentalis* does not occur with *H. powellianus* at the same locality. In the San Juan Basin, *Hyopsodus powellianus* is unknown. In the Piceance Basin, *Hyopsodus powellianus* may have replaced *H. sp.*, cf. *H. mentalis* (Kihm, 1984). The "gradually separating" pattern of *Hyopsodus* evolution coupled with intra- and intergeneric competition is not at odds with the general implications of this conclusion. In the case of *H. sp.*, cf. *H. mentalis*, better resolution may be hampered by too many geographic and stratigraphic gaps.

CONCLUSIONS

Two lineages of *Hyopsodus* existed during the Wasatchian and earliest Bridgerian of western North America. One of these lineages, *Hyopsodus paulus*, is common at all known localities and persisted after the Gardnerbuttean into the later Bridgerian. In order to describe more fully its pattern of change through time, *H. paulus* is divided into lineage segments. *Hyopsodus paulus*–*simplex*, the most primitive segment of *H. paulus*, is represented by specimens from the Sandcouleean and Graybullian. The anagenetically more progressive *H. paulus*–*lysiteensis* segment denotes late Graybullian through Lysitean *Hyopsodus paulus*. Lostcabinian and Gardnerbuttean populations of *Hyopsodus paulus* are named *H. paulus*–*wortmani* and *H. paulus*–*paulus*, respectively.

The second lineage, *Hyopsodus powellianus*, is much larger in tooth size and probably diverged from *H. paulus* in the Graybullian. It is not known from the Graybullian localities examined in this revision, but is distinct by the Lysitean. *Hyopsodus powellianus* (lineage segment *powellianus*) is very common in the Lysitean of the Wind River and Bighorn basins and continues through the Lostcabinian (as lineage segment *walcottianus*) in reduced numbers. One specimen records its youngest occurrence in the Gardnerbuttean of the Wind River Formation.

In this study, the diagnosis of *Hyopsodus loomisi* is expanded to include characters of the lower dentition as well as expected morphological variation similar to that of other *Hyopsodus* taxa. *Hyopsodus loomisi* co-occurs with *H. paulus* in the Sandcouleean and a large portion of the Graybullian.

The small *Hyopsodus minor* was possibly present by the mid- to late Graybullian of the Bighorn Basin and is known from the Piceance and San Juan basins. It coexisted with *H. paulus* and *H. powellianus* in the Lysitean of the Wind River and Willwood formations.

A second small species of *Hyopsodus*, closely tied to *H. paulus*–*wortmani*, is first distinguishable by the earliest Bridgerian (Gardnerbuttean). This species, *Hyopsodus minusculus*, is as common as *H. paulus*–*paulus* at CM loc. 34 in the uppermost Wind River Formation. CM loc. 34 represents the only Wind River

Formation locality where very large numbers of a small and intermediate lineage of *Hyopsodus* co-occur.

Other specimens have been morphologically allied under *Hyopsodus* sp., cf. *H. mentalis*, although its biostratigraphic record and geographic distribution suggest it may be an unnatural grouping.

Detailed investigation of CM material from the Wind River Basin (over 3000 catalogue numbers, approximately 6000 total specimens) confirms the presence of four taxa (not including the uncommon and thus far presumed immigrant *H. sp.*, cf. *H. mentalis*) of *Hyopsodus* in the early Lysitean through Gardnerbuttean—spanning what is now assumed to be between two to over three million years (Krishtalka et al., 1987). During this time interval, *H. minor* became extinct, *H. paulus* and *H. powellianus* evolved anagenetically, and one new taxon of *Hyopsodus*, *H. minusculus*, appeared. This does not appear to represent a rapid rate of cladogenesis within Wasatchian and early Bridgerian *Hyopsodus*. However, anagenesis affected the changing morphology of both *H. paulus* and *H. powellianus*. Anagenetic rate differed between the two lineages. For example, specimens of Lostcabinian *H. powellianus* are morphologically distinct from those of its putative Lysitean ancestor, whereas in the *H. paulus* lineage, Lostcabinian specimens are less so.

Given the relationships proposed here, the rate of cladogenesis is one taxon (in this case, *H. minusculus*) per two to 3.5 million years, or 0.29 to 0.50 (per million years). If “anagenetic taxa” are also considered new, then *H. powellianus*–*walcottianus* and *H. paulus*–*paulus* could be added to *H. minusculus*. The evolutionary rate would therefore increase to between 0.86 and 1.50. *Hyopsodus paulus*–*wortmani* is eliminated from these calculations because it is morphologically intermediate between *H. paulus*–*paulus* and *H. minusculus* and may represent biologically these two species at a very early stage.

For purposes of comparison with contemporaneous mammals, the Wasatchian Land Mammal Subage will be assumed to be six million years in duration (following figures 4.2–4.4 of Krishtalka et al., 1987). Four taxa of *Hyopsodus* evolved during this interval; this is an average and assumes *H. simplex* and *H. minor* are “conspecific” and that *H. sp.*, cf. *H. mentalis* is a distinct taxon in at least some of its referred distribution. The corresponding evolutionary rate is approximately 0.67. In light of the fact that this calculation does not account for lineage segments, it is best compared with the first estimate given in the preceding paragraph. This rate would not contradict the data of Gingerich (1974a, 1976b), assuming each of his tooth size lineages represent taxa similar to the species of this study. It has already been noted that dental evidence conflicts with Gingerich’s implied relationships in some cases, although the **number** of lineages is similar. The North American “Adapidae,” according to Gingerich (1979), seem to comprise four or five lineages in the Wasatchian and early Bridgerian as well. Taxonomic debates concerning the specific and generic assignments and implied taxonomy of these primates will continue (K. C. Beard, personal communication); however, the overall evolutionary rate and pattern of M_1 size change are analogous to that seen in *Hyopsodus*. Another possible connotation of this primate data will be discussed below. Krishtalka and Stucky (1985) report four lineages of *Diacodexis* in the Wasatchian, three showing relationship to the stem lineage *Diacodexis secans*, a rate of cladogenesis similar to that of *Hyopsodus*. *Hyracotherium*, a mammal as abundant as *Hyopsodus*, has not been revised through the entire Wasatchian since Kitts (1956). Unfortunately, this revision of *Hyopsodus* is not directly compara-

ble—Kitts believed that only upper premolar morphology was valid for taxonomic assignment and apparently only 500 or so specimens (this cannot be directly ascertained) were included in his analysis. Nevertheless, Kitts documented three species of *Hyracotherium* as well as five distinct subspecies marking temporal or geographic separation. The relationships of these taxa may be interpreted as representing three lineages: the large-sized *Hyracotherium craspedotum*, the smaller-sized *Hyracotherium angustidens*/*Hyracotherium vasaccience* lineage, and a *Hyracotherium vasaccience*/*venticolum*/*Orohippus* lineage (Kitts, 1956:55–57). The pattern of *Hyracotherium* lineage distribution through the Wasatchian is akin to that of *Hyopsodus*, as is the atypical size distribution of *Hyracotherium* reported by Kitts in the San Juan Basin horizons.

It has already been noted that several early Eocene omomyid primates show gradual change in dental morphology through time (Bown and Rose, 1987).

In contrast to these gradualistic patterns, a more abrupt dental evolutionary rate is evident in the artiodactyl *Bunophorus* (Stucky and Krishtalka, 1990) and the tilodont *Esthonyx* (Gingerich, 1980), for example. However, the number of specimens available for these revisions was only five percent of that known for *Hyopsodus*.

Hyopsodus may well be one taxon that, because of its abundance in the Eocene record, lends insight into change in mammalian dental morphology through time. As is often the case, greater knowledge in one area raises other questions of equal or greater magnitude. Would phylogenetic systematics have identified the emergent pattern of *Hyopsodus* evolution? In this case, it is clear that a cladistic analysis would not have done so. The integrity of a well-documented intermediate-sized lineage (one of the most commonly occurring fossil mammals known to paleontology) would have been broken into sister-group relationship with each of the *end members* of its various descendants. It would not remain a taxonomic entity, and the pattern of anagenetic evolution would have been lost or obscured.

Without critical understanding of the meaning and structural complexes of characters in their evolutionary context, cladistic analysis remains an exercise in gathering unrelated numerical data (Szalay, 1993). Evolutionary relationship and, therefore, phenetic distance is implied every time a character is thoughtfully weighed or assessed as primitive or derived. Without character assessment, cladism would merely be numerical taxonomy. Therefore, the “impartial data” resolved on cladograms *already* contains opinions of evolution. Gould (1991) seeks to resolve similar dilemmas by calling for the quantitative definition of morphospace, but gives no method of procedure. While this would undoubtedly resolve issues, it is probably a goal out of the paleontologist’s present reach.

There is no method of quantitatively measuring a character’s importance in reflecting phylogeny. “Consistency” or “retention” indices do not record change in size, shape, complexity, or location over time. Since this magnitude cannot be numerically assessed, the absolute number of characters supporting phylogenetic relationship also has little meaning. Character analysis and identification (before they are “counted”) are still in the qualitative—and, arguably, evolutionary—state at this time. For example, it seems reasonable at least to hypothesize that if *Hyopsodus* were a primate, generic distinctions would be made among phenotypes considered “species” in this review. It may be that Gingerich’s (1979) “Adapidae” and *Hyopsodus*, showing similar phylogenetic pattern, responded similarly to similar selection pressures, and thus should be considered comparable early Eocene biologic entities.

Should change be expected to be equal for comparable biologic units? Does the degree of change have systematic importance? For example, does the loss of a premolar in a primate taxon phyletically equal the inflation of M_{1-2} entoconid and hypoconulid in *Hyopsodus powellianus*? Is it more or less taxonomically important? Without common definition, it is difficult to ascertain whether fossil phena are genera, species, regional variants, or even equivalent.

The phylogenetic pattern of *Hyopsodus* begs the question: what biological process is actually being documented in studies of fossil organisms from basins that, while isolated, are in close approximation with one another? This will have to remain uncertain, but does not change the fact that a common pattern does exist. If, as this author suspects, this change represents gradual population genetic shifts around a constrained mean, with small scale immigrations of new taxa representative of cladogenetic events, does this still not represent an important evolutionary phenomenon? Simply because the pattern is termed anagenetic at this level of resolution does not have to imply the presence of sympatric speciation. The paleogeography of Eocene western North America indicates excellent isolating basins for small scale allopatry. Change does occur—*Hyopsodus* from Lysitean localities does not look like *Hyopsodus* from Bridgerian localities, even if little apparent cladogenetic evolution has occurred in this interval. Interesting things are happening more or less concurrently in other basins. Examination of *Hyopsodus* from new collections from the Uinta Basin (K. Doi, University of Colorado, personal communication) documents different “micropatterns” in *Hyopsodus* evolution. For example, large Washakie *Hyopsodus* seems to reduce accessory cusps rather than enlarge them.

The most valuable conclusions of this report are not the synonymies or the proposed relationships of the taxa of *Hyopsodus*. Rather, they are the observations of the variation in dental characters, the change in frequency of these characters, and the evolutionary pattern they suggest. The pattern of *Hyopsodus* evolution was not inferred after an “impartial” cladistic analysis but after the construction of a character evaluation grounded in a sequential, temporal lattice (see functional-adaptive analysis in Bock, 1981). Virtually no character was unequivocally exclusive to a specific *Hyopsodus* taxon. Relative time suggested pattern. Without it, no character could be unquestionably evaluated and weighed.

This study is therefore the result of the same type of phylogenetic evaluation employed by workers since the advent of paleontology. That is, the inspection of material in its temporal context, gain of a qualitative knowledge of the frequency and importance of morphologic features, and the inference of a pattern of change in this morphology (Szalay, 1993). These analytical threads are still basic to paleontological technique. Taxa defined by common principles can only improve the results of integrated studies of evolution, biostratigraphy, and paleoecology.

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A NOTE ON THE TRILOBITE GENUS *DIXIPHOPYGE*DAVID K. BREZINSKI¹

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ABSTRACT

Recovery of the first nearly complete thoracopygon of the trilobite genus *Dixiphopyge* Brezinski from the Chouteau Formation of central Missouri aids in evaluating the paleoecology and taxonomic affinities of this genus. *Dixiphopyge* is an isopygous trilobite, suboval in outline, and possessing nine thoracic segments. At the apex of each axial ring is a hollow tubercle that may represent the base of a short spine. *Dixiphopyge* inhabited muddy biostrome environments. In an enrolled position *Dixiphopyge* is interpreted to have looked somewhat like a porcupine with its spines radiating outward, presumably to inhibit its consumption by predators. Previous subfamily assignment of *Dixiphopyge* in the Otariioninae with *Cyphaspis* and *Namuropyge* may have been incorrect, because the latter two genera possess broad preglabellar fields and are micropygous.

INTRODUCTION

The genus *Dixiphopyge* was erected by Brezinski (1988) and is based on the trilobite species *Brachymetopus armatus* Vogdes (1891) from the Lower Mississippian Chouteau Formation of central Missouri. *Dixiphopyge* was based upon and described from co-occurring disarticulated cranidial and pygidial fragments, interpreted by Brezinski (1988) to belong to the same species. Recently, an articulated thorax with the pygidium and part of an eroded cephalon attached was recovered from the Chouteau of central Missouri. This new specimen provides insight into the taxonomy and paleoecology of the genus *Dixiphopyge* Brezinski.

The purpose of this note is to describe the new specimen of *Dixiphopyge*, which confirms the conspecific nature of the pygidia and cranidia previously known from disjunct fragments, and to discuss inferences about the paleoecology of this trilobite genus. The specimen herein described is repositied within the invertebrate paleontology collections at Carnegie Museum of Natural History (CM).

PALEOECOLOGY

Perhaps the single most important inference about the paleoecology of *Dixiphopyge armatus* can be gleaned from its paleoenvironmental distribution. Brezinski (1986) discussed the distribution of trilobite species from the Chouteau Formation of central Missouri and found that *D. armatus* consistently inhabited lime mud biostromes of the lower part of the Chouteau Formation. These mud biostromes are typically less than 10 ft in thickness and contain abundant fenestrate bryozoans (King, 1980). King (1980:18) likened these mud biostromes to incipient Waulsortian mud mounds. Tilsley (1977) documented the presence of the closely related spinose trilobite *Namuropyge* in a carbonate buildup in Great Britain. Likewise, Miller (1973) proposed that *Namuropyge* inhabited cryptic environments similar to those found in carbonate buildups. However, the Chouteau mud biostromes do not appear to have presented the diverse cryptic settings that

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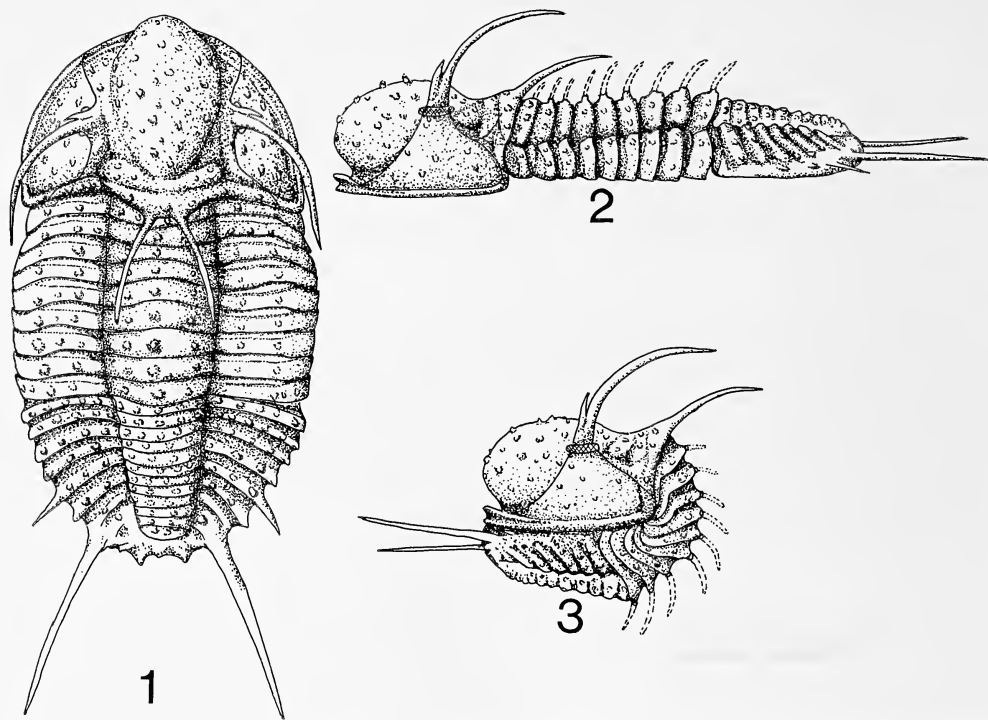


Fig 1.—1-3, reconstructed exoskeleton of *Dixiphopyge armatus* (Vogdes) in dorsal, lateral extended, and lateral enrolled views. Length and shape of axial spines is speculative.

were available in the carbonate buildups of Great Britain. In fact, the Chouteau buildups appear to have been more like mud mounds rather than reefs.

Inferences about the autecology of spinose trilobites such as *Dixiphopyge* have been numerous. Clarkson (1969) interpreted the Silurian odontopleurid trilobite *Leonaspis* as having utilized its radially directed, marginal spines as a means to inhibit sinking into soft substrate. Hahn et al. (1980) proposed a similar function for the marginal spines in *Namuropyge*. *Dixiphopyge* does not possess the large marginal spines which could be used in this way. Instead, the spines on *Dixiphopyge* are directed vertically and posteriorly (Fig. 1.2). These spines may have inhibited predators from seizing this species. In an enrolled position (Fig. 1.3) the spines may have effectively enlarged the size of the enrolled specimen making it more difficult to consume. It seems clear from the reconstruction shown in Figure 1.3 that in an enrolled position *Dixiphopyge*'s spines were more likely a defense mechanism rather than an adaptation to substrate conditions. Indeed, in an enrolled position *Dixiphopyge* is interpreted to have resembled a curled-up porcupine.

SYSTEMATIC PALEONTOLOGY

Genus *Dixiphopyge* Brezinski, 1988

Dixiphopyge armatus (Vogdes, 1891)

Fig. 1.1-1.3, 2.1-2.3

Brachymetopus armatus Vogdes, 1891:617-618, pl. 15, fig. 4, 5; S. Weller, 1898:149; Branson and Andrews, 1938:120, pl. 15, fig. 15-18; Shimer and Shrock, 1944:pl. 275, fig. 13-15.

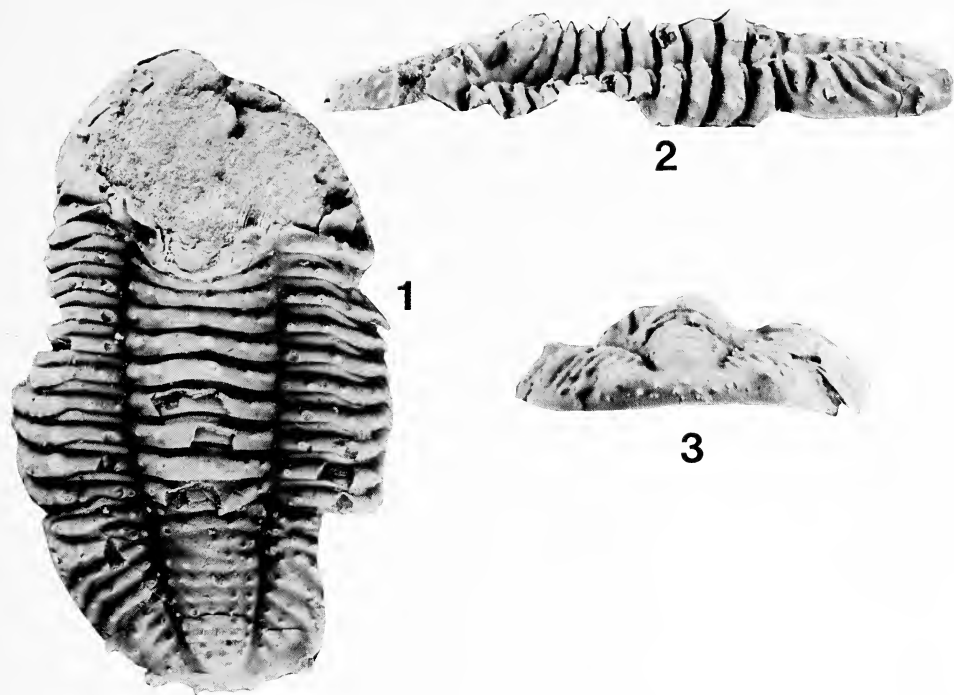


Fig. 2.—1–3, *Dixiphopyge armatus* (Vogdes). Dorsal, lateral, and posterior views of articulated thoracopygon collected from the Chouteau Formation, Boone County, Missouri; CM 35078; $\times 4.0$.

Brachymetopus sp. Branson and Andrews, 1938:115, fig. 11.

Namuropyge armata (Vogdes, 1891), Hahn, Hahn, and Brauckmann, 1980:pl. 2, fig. 9.

Namuropyge? *armata* Brezinski, 1986:878–879.

Dixiphopyge armatus Brezinski, 1988:104–105, fig. 2, 3.1–3.9.

New Material.—A single articulated thoracopygon with a mostly eroded cephalon from the lower Chouteau Formation near Providence, Boone County, Missouri, CM 35078.

Added Description.—Isopygous trilobite with exoskeleton suboval in outline. For cranial description, see Brezinski (1988:104–105). Lateral border furrow narrow, deep, border sharply rounded, tuberculate; genal angle broadly rounded; posterior border furrow shallowing adaxially, curved in transverse profile, steeply inclined abaxially; posterior border rounded.

Thorax composed of nine subequal segments; more anterior segments slightly smaller in transverse direction; pleurae rounded at fulcrum, steeply inclined abaxially, flattened adaxially; axial furrow sharp, shallow; pleural furrows deep, broad at fulcrum, shallowing adaxially and distally; pleurae rounded in longitudinal profile, ornamented posteriorly by three to four tubercles at the posterior apex; axial rings semicircular in transverse profile, rounded in longitudinal profile; ring furrows deep, wide, sinuous; rings ornamented by five tubercles, smaller adjacent to axial furrow, larger at ring apex; apical tubercles hollow, large, increasing in size posteriorly.

Pygidium moderately vaulted, subparabolic in outline. Axis of 11 rings, outline tapering moderately posteriorly; descending slightly posteriorly in longitudinal

profile; nearly reaching posterior terminus. Rings of low vaulting, semicircular in transverse and longitudinal profile ornamented by a row of five tubercles along apex; ring furrows shallow, narrow, rounded. Axial furrow shallow, narrow, curved along length. Pleural field of low vaulting, composed of eight ribs laterally directed in front, becoming curved and directed more posteriorly to the rear; ribs rounded in transverse profile, narrow, ornamented by a row of tubercles numbering five on first rib and one on rib number eight. Pleural furrows broad, moderately deep, rounded in longitudinal profile, shallowing posteriorly. Border indistinct, exhibits posteriolaterally directed spines opposite pleural ribs five, six, and eight; posterior terminus exhibiting six to seven small spines.

Remarks.—Although the cephalon is mostly eroded, the highly vaulted occipital ring and the course of the lateral portion of the occipital furrow and the lateral preoccipital lobes compare favorably with those described and illustrated by Brezinski (1988:104–105, fig. 2.1, 3.1–3.4, 3.9). The pygidium is nearly identical to that of *D. armatus* (Vogdes) as illustrated by Brezinski (1988:fig. 2.3, 3.5–3.8), differing only in the distal bifurcation of the second anteriormost pleural rib on the left side. This is interpreted as a teratological manifestation inasmuch no such bifurcation is evident in those specimens illustrated by Brezinski (1988:fig. 3.5–3.8) and, therefore, probably has no taxonomic significance.

Taxonomic Affinities.—Brezinski (1988) proposed that *Dixiphopyge* was closely related to members of the Otarioninae such as *Cyphaspis* and *Namuropyge*. Recently, Adrain and Chatterton (1994) expressed uncertainty regarding the closeness of this relationship. Indeed, members of the subfamily Otarioninae are diagnosed by the presence of a preglabellar field and typically are micropygous. *Dixiphopyge* lacks any preglabellar field and is clearly isopygous. Although other characters such as the bulbous glabella and pronounced spinosity are compatible with the Otarioninae, *Dixiphopyge* might well be assignable to a separate subfamily of which it is the only currently known member.

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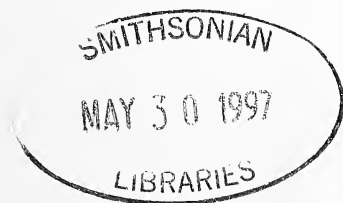
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THE CARNEGIE
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LIFE ON THE EFFECTIVE BUBBLE:
EXOCRINE SECRETION DELIVERY SYSTEMS (ESDS) AND
THE EVOLUTION AND CLASSIFICATION OF
BEETLES IN THE FAMILY HYDRAENIDAE
(INSECTA: COLEOPTERA)

PHILIP D. PERKINS¹

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ABSTRACT

Exocrine secretion delivery systems (ESDS) of aquatic beetles in the family Hydraenidae are described for the first time, and used to clarify phylogenetic relationships within the family. ESDS components include secretion-grooming behavior, surface cuticular specializations for secretion delivery, locations of exocrine pores, and locations and densities of ductules and end-apparatus of exocrine glands. ESDS structures are illustrated with scanning electron micrographs and drawings. The systems function, at least in part, to maintain the respiratory bubble by making the cuticular surfaces within the bubble, and especially at critical marginal areas of the bubble, clean of hydrophilic microbes and debris. Secretion-grooming is performed out of the water, often with the beetle "on edge," the legs on the "free" side acting together in patterns of secretion spreading and mutual rubbing. Spreading of secretions on the cuticular surface, movement of secretions between body areas, and cleaning of the cuticle by scraping and rubbing are achieved by specialized patches and rows of setae on the legs.

A reclassification of the family is proposed, based in large part on putative synapomorphic characters and morphoclines of the ESDS and antennal pocket. The following suprageneric taxa are proposed and characterized: Orchymontinae, new subfamily; new tribes Madagastriini, Parhydraenini, and Ochtheosini; and new subtribes Meropathina, Neochthebiina, Protochthebiina, and Enicocerina. In the Ochthebiinae, the "subgenera" *Calobius* Wollaston, *Cobalius* Rey, *Liochthebius* J. Sahlberg, and *No-tochthebius* Orchymont are reduced to synonymy with *Ochthebius*, whereas full generic status is proposed for *Aulacochthebius* Kuwert and *Enicocerus* Stephens. In the Hydraeninae, *Hydraenopsis* Janssens and *Spanglerina* Perkins are synonymized with *Hydraena* Kugelann, whereas *Haenydra* Rey and *Hadrenya* Rey are considered valid subgenera.

The following new genera and new species are described: *Haptaenida huggerti* (Ecuador), *Madagaster steineri* (Madagascar), *Ochtheosus fungicolus* (Chile), *Protochthebius satô* (Nepal), *Protozantaena labrata* (South Africa), *Pneuminion velamen* (South Africa), and *Tympallopattrum longitutum* (Australia). *Davidraena bacata* n. sp. is described from India. Keys to the subfamilies, tribes, and genera of Hydraeninae, and tribes, subtribes, and genera of Ochthebiinae are given.

INTRODUCTION

Microhabitats, Behavior, and Morphology

Members of the family Hydraenidae are tiny beetles, the majority of which are adapted for marginal life in the microscopic aquatic world. These aquatic beetles breathe by means of an air reservoir covering the ventral surface. Hydraenids cannot swim, but are able, due to their small size and ventral bubble, to "walk," upside down, on the water's surface film. The respiratory bubble is pivotal to the ability of these beetles to effectively utilize the microaquatic world. This paper describes the varied and intricate ways that the hydraenid bubble is formed and

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maintained, and uses these new character systems to clarify relationships and classification of the family.

Hydraenid beetles live in a wide variety of aquatic habitats. Although most species live at the sandy-gravelly margins of streams and ponds (Perkins, 1981), some species live in stagnant water (Cuppen, 1993), a very small percentage of the species are semiaquatic or humicolous (Perkins and Balfour-Browne, 1994), and one species, described herein, is fungicolous.

Three hydraenid genera, *Ochthebius*, *Hydraena*, and *Limnebius*, have specialized "exocrine secretion delivery systems" (ESDS), described below, that help maintain the respiratory bubble. Members of these three genera, while out of the water, perform a series of secretion-grooming motions with the legs. The leg actions, principally repetitive movements of the femora and tibiae, correlate with the locations of exocrine gland pores and associated cuticular elements such as specialized setae, cuticular ridges, and secretion grooves.

In *Hydraena* and *Limnebius* the full repertoire of secretion-grooming is performed with the beetle "on edge" (Fig. 9A, 25A), with the legs on one side "in the air," acting in complicated concert to perform the spreading, transferral, and cleaning actions. This behavior not only spreads the secretions, it also coordinates the evolution of ESDS components located on different body regions.

The genera *Ochthebius*, *Hydraena*, and *Limnebius*, are conspicuously "successful"; that is, they are by far the most speciose in the family and are cosmopolitan, or nearly so, in distribution (Fig. 71). The ability to make the cuticle resistant to wetting within, and especially at critical marginal areas of the respiratory bubble, is obviously a necessary prerequisite for effective utilization of aquatic habitats by hydraenids. It seems likely, therefore, that the possession of a specialized ESDS is a major reason why these three genera have attained relative success in the family. Plesiomorphic (and less successful) genera lack specialized ESDS.

ESDS components (i.e., locations, structures, and behavior) of *Ochthebius*, *Hydraena*, and *Limnebius* differ markedly one from the other. This evidence strongly suggests that ESDS specializations for aquatic existence evolved independently in these three genera, each from a different, less specialized ancestor. Whether these ancestors were aquatic, semiaquatic, or perhaps even humicolous, is an open question. The habits of the common ancestor of the family are an even more remote question, but the likelihood of humicolous habits seems to be increased by these findings.

In addition to the bubble maintenance components, ESDS also include exocrine glands that secrete onto the wet portions of the cuticle (i.e., outside the bubble). The locations, end-apparatus, and pore distributions of some of these glands are described, and some probable functions of the secretions are discussed below. Variations in ESDS within taxa are shown to be very effective in clarifying some long-standing systematic problems, especially in the Ochthebiinae.

In most insects the antennae serve only olfactory and sometimes tactile functions. In hydraenids the antennae also serve as part of the respiratory system: they are used to break the water's surface film so that the air reservoir ("bubble") can be replenished. The last five articles of the antenna form a "club" that, in addition to having olfactory sensilla, is clothed in hydrofuge hairs and therefore water repellent (Fig. 1A).

When not performing its essential and often repeated act of being raised to break the surface film, the antenna is held beneath the eye, with the club protected

by being placed behind the eye and/or in the "antennal pocket" of the adjacent prothorax (Fig. 2, 19A). Exocrine glands and cuticular areas behind the eye and on the prothorax have evolved together, resulting in an integrated system that (1) protects the antennal club, (2) helps maintain the respiratory bubble, and (3) provides sensory receptors for molecules brought into the postocular area by the antennal club.

The complexities of the antennal pocket vary among the taxa, providing many previously undescribed characters that are essential to a better understanding of the evolution and classification of the family.

Functions of Exocrine Secretions

Studies of aquatic beetles in other families, such as the diving beetles (Dytiscidae) and related adephagan families, have shown that some exocrine gland secretions are hydrophilic and serve as wetting agents in addition to being antimicrobial (Dettner, 1985). The beetle's cuticle, when not coated with a secretion, is hydrophobic; this water-repellant condition can prevent tiny beetles from breaking through the surface film to enter the water (Dettner and Schwinger, 1980). This hydrophobic state is changed to a hydrophilic one by the beetles (while out of the water) using the legs to spread hydrophilic exocrine secretions over the body surface. The air reservoir in these adephagan beetles is under the elytra, and the entire body surface (except the abdominal apex) is wet when the adult is in the water.

In contrast to adephagan aquatic beetles, many aquatic bugs have ventral hydrofuge hairs that hold an air reservoir. Recently Kovac and Maschwitz (1989, 1991) gave experimental evidence that the exocrine secretion produced by the metathoracic gland of aquatic bugs (Pleidae, Corixidae, Naucoridae) functions to kill bacteria. The hydrofuge hairs become wettable if covered with hydrophilic bacteria, the respiratory bubble is consequently lost, and the animals drown. The secretion, consisting principally of hydrogen peroxide, is rubbed on the hydrofuge pubescence by the legs. Kovac and Maschwitz (1989, 1991) termed this behavior "secretion-grooming."

Hydraenid beetles differ markedly from aquatic adephagan beetles (i.e., dytiscids) and aquatic bugs in both basic structural morphology and behavior. Dytiscids and aquatic bugs are very active swimmers, whereas hydraenids cannot swim, but instead crawl over the substrate. Hydraenids have a ventral air bubble, but replenish it by using the antennae to form an air funnel to the surface, instead of using the tip of the abdomen. The secretion-grooming behavior of hydraenids is very different from that of aquatic bugs, and the secretions lack any indication of "foaming" like that produced by hydrogen peroxide secretions.

Although tests of the physicochemical properties of the secretions produced by hydraenids have not been made, it seems reasonable to assume a hydrophilic nature for chemicals that are secreted onto surfaces that are wet when the beetle is in the water (i.e., surfaces outside the bubble). Since insect cuticle is hydrophobic, wettability via secretions is essential to prevent these tiny beetles from becoming "trapped" in the water's surface film. In contrast, secretions produced onto surfaces within and at the margins of the respiratory bubble certainly cannot be hydrophilic, but must be hydrophobic.

Antimicrobial (i.e., defensive) properties are also expected for hydraenid exocrine secretions, as was demonstrated for dytiscids, etc., by Dettner and Schwinger

(1980). The hydrogen peroxide secretion of aquatic bugs is effective against bacteria but ineffective against protozoa (sessile ciliates) that colonize only the wet parts of the cuticle (Kovac and Maschwitz, 1989). The sessile ciliates' nonsusceptibility to the antiseptic secretion does not impair the bugs' respiration, because the ciliates attach outside the respiratory bubble. However, protozoa attaching to or at the bases of setae that function to maintain a special part of the bubble, such as adjacent to the antenna in hydraenids, could have negative effects on respiration and on chemoreceptive functions integrated with the air capture system.

Over the past 20 years there has been a steady increase in knowledge of defensive exocrine secretions of Coleoptera (Dettner, 1987). However, these studies have involved a relatively small part of the order. About 175 families of Coleoptera are currently recognized (Crowson, 1981; Lawrence and Newton, 1995). Of these, only about 32 families have had some representatives studied for the comparative distribution of exocrine glands and the chemistry of their secretions (Dettner, 1987). Of these 32 families, only about ten have had the adult stage of some species studied by three methods, that is, SEM (for associated surface structures), histological/cytological preparations, and chemical analysis of secretions.

Several of the genera that have been studied are members of huge families (e.g., Staphylinidae, Tenebrionidae, Scarabaeidae, Chrysomelidae), and can scarcely represent the immense bio- and morphodiversity of these families. The matter of function is further clouded since glands with similar cytology have been found to secrete very different chemicals. Functions of exocrine secretions can be as diverse as sex pheromones in successive behavior patterns, defensive repellants, organic carriers, surfactants, penetrators, evaporation retardants, water repellants, and antimicrobials.

Even cockroaches, with perhaps the best studied glandular exocrine systems, are replete with unknowns. For example, Brossut (1983) identified 43 exocrine products from only ten cockroach species, and emphasized that functions could not be assigned to most of those chemicals in the absence of behavioral studies.

Of the Coleoptera exocrine systems described in the literature, I was unable to find any that are similar to those of hydraenids. Taxa included in this review are: Anisotomidae (Cazals and Juberthie-Jupeau, 1983); Anobiidae (Levinson et al., 1983); Bruchidae (Biemont et al., 1990); Carabidae (Forsyth, 1970; Juberthie and Piquemal, 1977); Catopidae (Martin, 1977); Chrysomelidae (Kendall, 1972); Dermestidae (Hammack et al., 1973); Dytiscidae (Forsyth, 1968; Dettner and Schwinger, 1980; Dettner, 1985); Gyrinidae, Haliplidae, and Noteridae (Forsyth, 1968); Pselaphidae (Cammaerts, 1974; Hill et al., 1976); Pyrochroidae (Dettner, 1984); Scarabaeidae (Pluot-Sigwalt, 1986, 1991); Scolytidae (Happ et al., 1971); Staphylinidae (Pasteels, 1968a, 1968b, 1969; Araújo, 1978; Peschke, 1978, 1986; Klinger, 1980; Araújo and Pasteels, 1987; Peschke and Metzler, 1987; Dettner and Reissenweber, 1991; Johannes et al., 1993); Tenebrionidae (Roth, 1943; Wigglesworth, 1948; Roth and Eisner, 1962; Eisner et al., 1964; Delachambre, 1973; Tschinkel, 1975a, 1975b; Tschinkel and Doyen, 1980).

Purpose and Organization

The purposes of this paper are to describe in detail previously unknown character systems, including behavioral components, of the specialized ESDS of the genera *Ochthebius*, *Hydraena*, and *Limnebius*; describe and compare cuticular parts of corresponding body regions in all genera of the family; and apply the results of the comparative morphological study to the classification of the family.

The general organization of the paper is as follows: (1) the secretion-grooming behavior and functional anatomy of the ESDS of *Ochthebius*, *Hydraena*, and *Limnebius* are described; (2) a revised classification of the family is presented, including descriptions and discussions of the ESDS and corresponding cuticular parts and body regions in all genera and subgenera, discussion of plesiomorphic and putative synapomorphic character states, and formal descriptions of new taxa; (3) taxonomic keys utilizing the new character systems are provided; and (4) concluding remarks are given.

A list of the taxa that were studied in transparency mounts, and designations of new combinations, is given in Appendix 1. An index to the major topics is given in Appendix 2.

MATERIALS AND METHODS

Microtechniques

Specimens were prepared for transparency mounts by the following steps: (1) dry specimen placed in 10% potassium hydroxide at room temperature; (2) after appropriate maceration with potassium hydroxide (usually overnight), specimen transferred to a 3% solution of hydrogen peroxide; (3) after appropriate decolorization in hydrogen peroxide (usually minutes), specimen transferred to distilled water; (4) after at least 30 minutes in distilled water, specimen transferred to 80% ethanol for a few minutes, and then into 95% ethanol; and (5) after air bubbles have disappeared, specimen transferred to 80% ethanol for a few minutes (or temporarily stored in 80% ethanol).

Cleared and decolored specimens were studied with a compound microscope, either as depression slide preparations in lactic acid (and later stored in glycerin on microslides), or slide mounted in balsam, using standard techniques. Some specimens were stained with acid fuchsin before being studied in transparency mounts.

Specimens used for scanning electron microscopy were cleaned in a sonic cleaner (in 80% ethanol), then dehydrated in 95% ethanol before being placed in acetone (for a few minutes). In a few instances, specimens that had been studied as transparency preparations were subsequently removed from microslides, cleaned, and studied by SEM, thereby allowing a one-to-one correlation between internal and surface structures.

Illustrations of male genitalia and other body parts were prepared with the aid of a drawing tube attached to a compound microscope, using temporary transparency mounts in lactic acid. For storage, the aedeagus and dissected body parts of each specimen are in glycerin in a glass microvial which is affixed to the pin of the specimen.

Acronyms of Structures

The following acronyms are used for external cuticular features: **ah-border**, anterior hyaline border of the pronotum; **gap-setae**, genal antennal pocket setae; **hap-setae**, hypomer al antennal pocket setae; **hh-border**, hypomer al hyaline border; **hp-sensilla**, hypomer al paired sensilla; **hsd-carina**, hypomer al secretion delivery carina; **hsd-sulcus**, hypomer al secretion delivery sulcus; **hsd-surface**, hypomer al secretion delivery surface; **lh-border**, lateral hyaline border of the prothorax; **pa-groove**, postocular antennal groove of the head; **psd-setae**, postocular secretion delivery setae of the head; **psd-sulcus**, postocular secretion delivery sulcus of the head; **sa-groove**, subocular antennal groove of the head.

SECRETION-GROOMING BEHAVIOR AND FUNCTIONAL ANATOMY

Genus Ochthebius

Secretion-grooming Behavior.—The secretion-grooming behavior of *Ochthebius* described below is based on observations of two distantly related species from North America, *O. (sensu stricto) interruptus* and *O. (Asiobates) puncticollis*. Aspects of the biology and taxonomy of these species are given by Perkins (1976, 1981).

Given the behavioral similarities observed in these two species, and given the phylogenetic distance separating them, it is perhaps reasonable to expect similar behavior in most species of the genus that have similar specialized exocrine structures and similar leg morphology. Of course observations of many other species are necessary to confirm this prediction.

The individuals of *Ochthebius* observed thus far did not position themselves "on edge," as is described below for *Hydraena* and *Limnebius*. Rather, the body is raised and balanced on some of the legs, while the "free" legs perform the secretion-grooming.

One of the first actions in secretion-grooming is the extension and deflexion of the prothorax. This action opens the hydrofuge area surrounding the mesothoracic spiracles, allowing the removal of water and any other contaminants. As described below, much of the leg actions take place in the hydrofuge area at the juncture of the prothorax and the mesosternum. The intersegmental membrane separating these two areas contains the large mesothoracic spiracles.

Often the prothorax is twisted from side to side, and sometimes "pulsates" in a deflexing motion. Sometimes the head is pressed upward against the anterior hyaline border (while the pronotum is deflexed). These actions probably move water to areas where it can be removed and/or will evaporate more rapidly.

Two kinds of movements of the front leg result in rubbing against the postero-ventral angle of the eye. In this location are specialized (shaped like eyelashes) postocular secretion delivery setae (henceforth termed psd-setae) that are adjacent to a secretion reservoir, the postocular secretion delivery sulcus (= psd-sulcus; e.g., Fig. 1). These rubbing actions may occur while the beetle is balanced on a total of three (the "tripod"), four, or five legs.

Usually the initial secretion-grooming leg behavior ("step 1") is a repeated probing at the area of the psd-setae with the spines at the apex of the protibia. This action surely causes a spreading of the exocrine secretion onto the protibial apex; it probably additionally forces more secretion out of the psd-sulcus by pressing against and deforming the thin cuticular rim. Sometimes, after the probing, the protibia is rubbed against the prosternum.

The second kind of leg behavior resulting in rubbing the psd-setae ("step 2") occurs when the protibia strokes across the top of the eye: at the end of this motion the distal area of the profemur comes into contact with the psd-setae. The area of the profemur that rubs the psd-setae is armed with stout setae, forming the "distal spine cluster" (Fig. 5).

Immediately after rubbing the psd-setae, the profemur is brought backward and the distal spinose area is rubbed ("step 3") against the ventral surface of the posterolateral area of the prothorax, where the lateral and the hypomerall hyaline borders are contiguous (e.g., Fig. 31).

The repeated action of rubbing the profemoral distal spine cluster against the psd-setae (step 1), and then *immediately* rubbing the hyaline borders at the hind

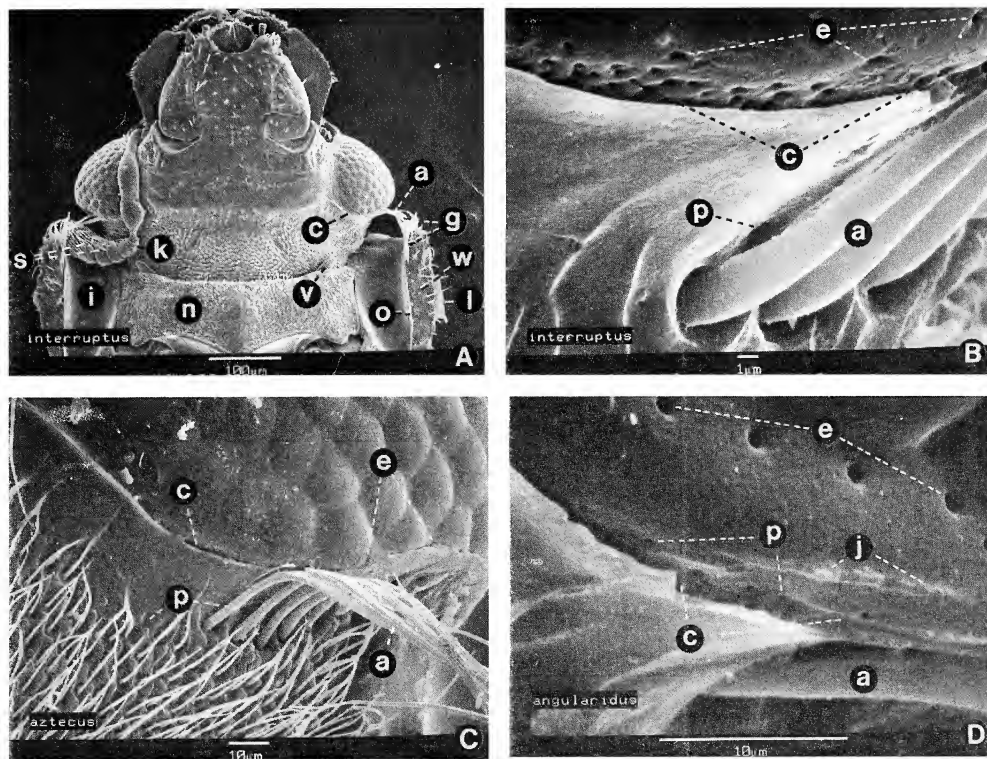


Fig. 1.—*Ochthebius*, venter of head and prothorax, and details of psd-sulcus area. A, B. *O. interruptus*. C. *O. aztecus*. D. *O. angularidus*. Structures: (a) psd-setae, (c) psd-sulcus (rim broken off in D), (e) pericocular exocrine pores, (g) hap-setae, (i) hypomeral antennal pocket, (j) cuticular ridge, (k) cupule article of antenna, (l) lh-border, (n) prosternum, (o) hh-border, (p) exocrine pores in psd-sulcus, (s) sensilla of antennal club, (v) cervical sclerite, (w) wet-hypomeron.

angles of the prothorax (step 2), surely results in the transferral and spreading of the exocrine secretions present on the psd-setae and in the psd-sulcus. Cleaning surfaces of debris and microbes certainly also occurs during these movements, by scraping with the stiff spines on the profemur.

Another distinct rubbing behavior (the “backstroke”) involves the middle legs, and occurs while the beetle is balanced on one (see below) or both of the front legs, and both of the hind legs. The middle legs, usually in unison, are brought forward until the femur of each is held tightly against the cuticle beneath the posterolateral angle of the pronotum (i.e., against the lateral hyaline border and posterior extreme of hypomeral hyaline border); the mesotibiae also are held tightly against the cuticle. The middle legs then extend posteriorly, again usually in unison. During this stroke the mesofemur rubs against the lateral part of the mesosternum, and the mesotibia rubs against the metasternum and/or the elytral epipleuron, especially the hydrofuge pubescent anterior part of the epipleuron.

Sometimes the actions of the middle legs and one front leg are integrated. During this behavior (the “tripod”) the beetle balances on three legs, one front and the two hind legs. While in this balanced position, the middle legs perform the “backstroke.” Concurrently, the “free” front leg performs the step 2 and then step 3 behaviors (sometimes, but not always, preceded by step 1).

After step 3, the front leg then engages in rapid mutual rubbing with the adjacent middle leg ("step 4"). Most of this mutual rubbing involves the femora, but the tibiae are also rubbed together. Initially the opposing faces of the two legs are rubbed together, but the legs are often "crossed over" and rubbed on the other faces. Sometimes the mesotibia is placed on top of the profemur, and rubs back and forth against the distal spine cluster. The opposing faces of the femora (posterior of profemora and anterior of mesofemora) each have a cluster of spinose setae (Fig. 5, 6) that are involved in this mutual rubbing.

Sometimes during step 4 (mutual rubbing) the pro- and mesofemora are alternately pressed tightly against and rubbed back and forth in the hypomeral/lateral hyaline border area. Like the profemur, the mesofemur has a distal spine cluster (Fig. 6) that contacts the hypomeral area during this behavior. During the "tripod," the step 2-3-4 behavioral sequence of the front leg is repeated several times while the middle legs are repeating the "backstroke" pattern.

The hind legs do some rubbing of the elytral epipleura, and often do mutual metatibial rubbing; the latter behavior is performed while the beetle is balanced on the front and middle legs. While stroking the elytral epipleuron, the metatibial spines probably also stroke the abdominal hydrofuge pubescence bordering the epipleuron. No extensive rubbing of the upper surface of the elytron was observed.

Following is a summary of the secretion-grooming leg movements: step 1: protibial apex probes at the psd-setae on the postocular area; step 2: protibia strokes across the dorsal surface of the eye, and at the end of this motion the distal spine cluster of the profemur rubs the psd-setae; step 3: distal spine cluster of the profemur rubs back and forth against the ventral surface of the hypomeral and lateral hyaline borders at the posterolateral area of the prothorax; step 4: profemur and protibia rub against the mesofemur and mesotibia of the adjacent middle leg; backstroke: middle legs, usually in unison, stroke backward; tripod: beetle balanced on one front leg and the two hind legs while "free" front leg and middle legs perform secretion-grooming behavior.

ESDS Cuticular Components.—In *Ochthebius* the postocular area and the hypomeral antennal pocket form a complex region of integrated structures (Fig. 1, 2). These structures include exocrine pores, secretion collecting reservoirs, secretion delivery setae, various forms of cuticular hydrofuge, thin hyaline margins, and the antenna.

The locations of these structures, and observations on living beetles (described above), strongly suggest that these structures function, at least in part, to help maintain the respiratory bubble around the antennal club. This is a critical marginal part of the bubble, an area that is subject to loss of hydrofuge properties resulting from the repeated movement of the antenna in and out of the bubble during air capture.

Antennal Pocket and Hyaline Borders.—A characteristic feature of the genus *Ochthebius* is the presence of thin, flexible, transparent hyaline borders on the prothorax (Fig. 28, 31). All species of the genus (as herein defined) have four hyaline borders: anterior (ah-border), posterior (ph-border), lateral (lh-border), and hypomeral (hh-border). Very rarely, the lh-border may be rudimentary or perhaps secondarily lost. Equally rarely, the entire pronotum may be margined with a hyaline border, the lh-border being continuous with the ah- and ph-borders.

The antennal pocket of the prothorax, in which the antennal club is held, is bordered by two hyaline margins, the ah-border that forms the anterior margin of

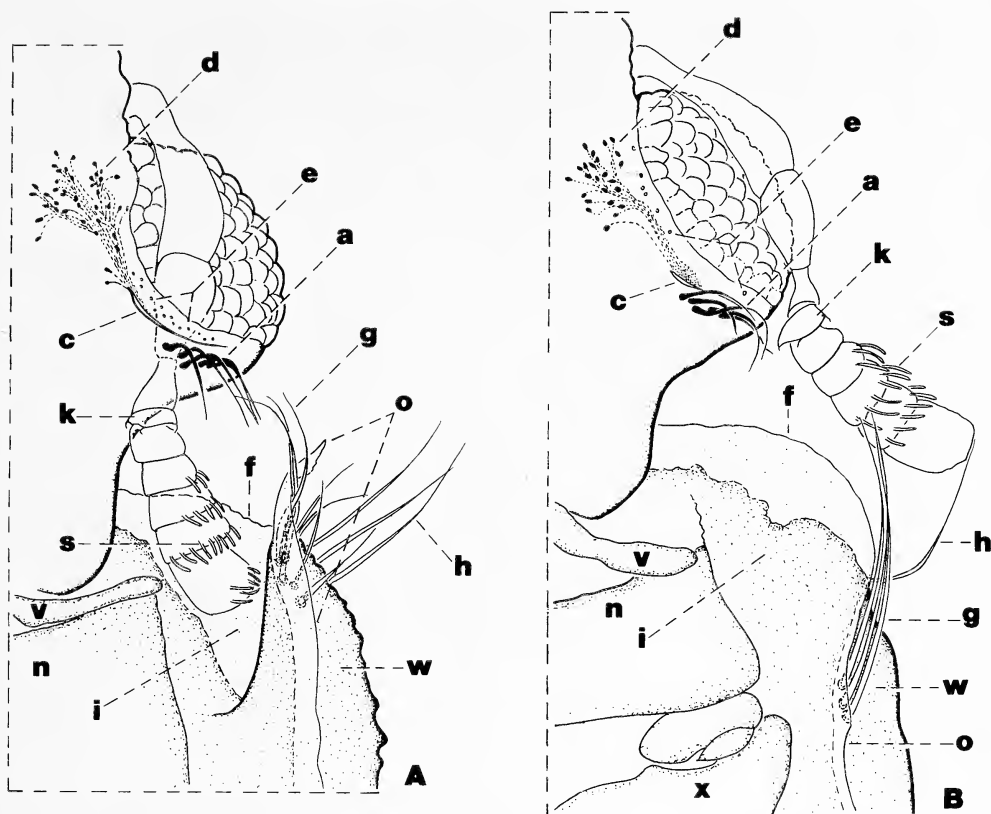


Fig. 2.—*Ochetidae*, ventral aspect of left side of head and adjacent area of prothorax, showing external cuticular features and internal end-apparatus and ductules (d) of exocrine glands. A. *O. glaber*. B. *O. quadricollis*. Structures: (a) psd-setae, (c) psd-sulcus, (d) end-apparatus and ductules of exocrine glands, (e) pericircular exocrine pores, (f) ah-border, (g) hap-setae, (h) anterolateral pronotal setae, (i) hypomerall antennal pocket, (k) cupule article of antenna, (n) prosternum, (o) hh-border, (s) sensilla of antennal club, (v) cervical sclerite, (w) wet-hypomeron, (x) procoxa.

the antennal pocket, and the hh-border that forms the lateral margin of the antennal pocket (Fig. 2:f, o). In many species these two hyaline margins are contiguous at the anterolateral angle of the prothorax (e.g., Fig. 28C).

The ventrally located hh-border (o in Fig. 1, 2, 28) forms the lateral limit of the prothoracic part of the respiratory bubble. The hh-border gradually reduces in height toward the posterior part of the hypomeron, and in its posterior part becomes contiguous with (but perpendicular to) the lh-border. Often the hh-border is indicated dorsally on the lh-border by a corresponding, shallowly impressed line.

The hh-border separates each hypomeron into two areas (Fig. 1, 2, 28): the lateral area (outside the bubble) that can be termed the wet-hypomeron (w), and the medial area that consists of the antennal pocket (i) and the postcoxal projection (Fig. 28:d) of the pronotum (the antennal pocket and the postcoxal projection can be jointly termed the bubble-hypomeron).

The lh-border is located posterolaterally (at least), its posterior extreme being contiguous with the ph-border. The degree of development and the shape of the

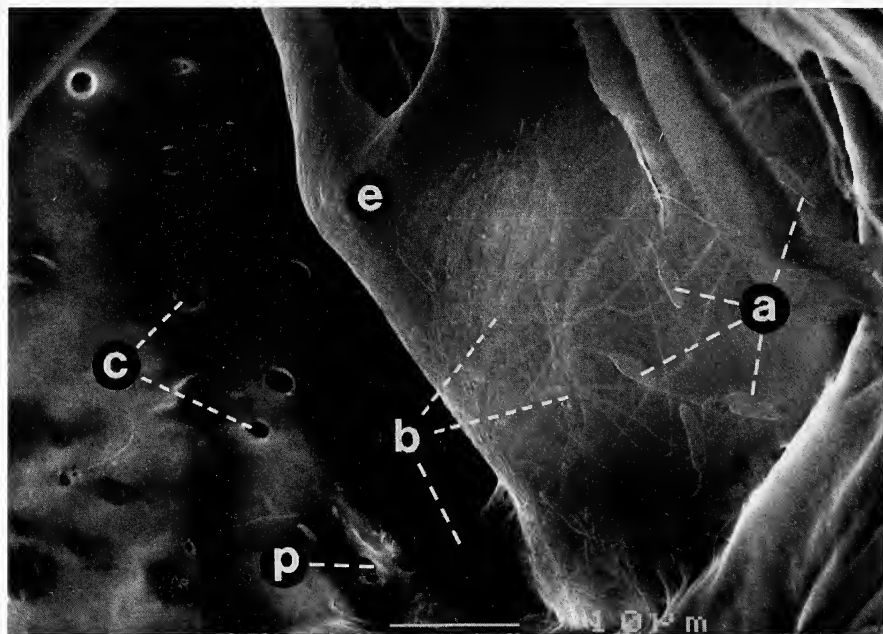


Fig. 3.—*Ochthebius gruwelli*, internal view of head (macerated with sodium hydroxide). Structures: (a) end-apparatus of exocrine glands, (b) ductules, (c) sockets of psd-setae, (e) cuticle of internal wall of eye, (p) internal surface of psd-sulcus.

lh-border varies among the species; usually the border occupies about the posterior one-half. The ah-border and the ph-border form the anterior and posterior margins of the prothorax respectively and (when the prothorax is moved such that gaps exist between the ah-border and the head, or the ph-border and the elytra) form the anterior and posterior margins of the bubble.

Peri- and Postocular Exocrine Pores.—Exocrine pores near the margin of the eye are of two types based on differences in size, positions, and internal cuticular components. These two types can be termed periocular pores and postocular pores.

Periocular pores are about $1.0\ \mu$ in diameter (about twice as large as postocular pores) and are located around the periphery of the eye (e.g., Fig. 1:e). Transparency whole-mount preparations do not show end-apparatus and ductules leading to these pores, suggesting that the associated glands are probably Type I (Noirot and Quennedey, 1974, 1991). Periocular pores are present in all hydraenids that have been studied, and are therefore probably an ancestral condition.

Postocular pores are smaller, about $0.5\ \mu$ in diameter, and are clustered near the posteroventral angle of the eye (e.g., Fig. 1B, D). Internally each of these pores is connected to a long ductule which terminates in a sperm-shaped end-apparatus (Fig. 2A:d, B:d; 3:a). The exocrine glands supplying these pores are therefore Type III (Noirot and Quennedey, 1974, 1991).

In many species groups the periocular pores are situated on a shelf-like area, and are distinctly separated from the postocular pores (e.g., Fig. 1D; 29B, D). In some species groups the shelf-like area is lacking and the two types of pores are adjacent to one another (e.g., Fig. 1B, C). This latter condition may be correlated

with overall eye shape (i.e., species with more convex eyes lack the shelf-like area).

Postocular Secretion Delivery Sulcus.—In members of *Ochthebius* the postocular pores are located in a secretion reservoir, the postocular secretion delivery (psd-) sulcus (e.g., Fig. 1B, D). The psd-sulcus is formed between the angulate margin of the eye and a thin cuticular ridge. If this ridge is broken, the postocular pores are revealed within the psd-sulcus (e.g., Fig. 1D).

Postocular Secretion Delivery Setae.—Immediately posterior to the psd-sulcus is a group of specialized setae, the postocular secretion delivery (psd-) setae (e.g., a in Fig. 1C, 2A). The psd-setae are bent adjacent to the psd-sulcus such that the secretion in the psd-sulcus spreads along the setae (spreading aided by antennal movements and grooming behavior with the front legs). In some SEM preparations (uncleaned specimens) the psd-setae are coated with the secretion (e.g., Fig. 1C). The psd-setae take various forms that are indicative of generic limits (see below).

Hypomerai Antennal Pocket Setae.—In *Ochthebius* the tips of the psd-setae are in contact with the tips of setae arising on the prothorax, the hypomerai antennal pocket (hap-) setae (e.g., g in Fig. 2A, B; 28C). Secretions on the psd-setae would presumably be spread onto these prothoracic setae by the antenna as it moves in and out of the antennal pocket, and/or by leg movements during grooming behavior.

Hypomerai Exocrine Glands.—Solitary (nonclustered) exocrine pores are found in the antennal pocket and on the wet-hypomeron. In the nonhydrofuge pubescent part of the antennal pocket the pores vary in density, but usually are quite sparse, although often slightly denser adjacent to the hypomerai hyaline border (Fig. 4B, C). In most species of *Ochthebius* (sensu stricto), pores are also sparse on the wet-hypomeron (for example, in *O. marinus* there are about 8–12 pores on the wet-hypomeron) and solitary, and lack large or obvious (in whole mounts) end-apparatus. In contrast, the wet-hypomeron of some species of *Enicocerus*, *Gymnochthebius*, and *Ochthebius* (*Asiobates*) have clusters of exocrine pores that are supplied with well-developed end-apparatus (Fig. 35C, D; 36C, D; 51A, B, C;—see discussion under *Enicocerus*).

Femoral Setae.—The femoral setae of two species, *O.* (sensu stricto) *interruptus* and *O.* (*Asiobates*) *puncticollis* are illustrated (Fig. 5–8). These two species differ in microhabitat, *O. interruptus* being found at or close to the waterline, whereas *O. puncticollis* is often found farther away from the waterline, on sandy-gravelly stream banks (Perkins, 1976).

These ecological differences correspond with differences in the femoral setal morphology. In *O. interruptus*, the “more aquatic” species, the femora have numerous elongate and flexible setae, placed near the margins of the pro- and mesofemora (Fig. 5A, 6A), and generally distributed over the anterior (substrate) face of the metafemur. In marked contrast, the meso- and metafemora of the less aquatic *O. puncticollis* lack these elongate, slender setae, instead having the anterior (substrate) surfaces with numerous, short, and stout setae (Fig. 6B, 8). In addition, the pro- and mesofemora of *O. puncticollis* have more setae in the distal spine cluster.

It seems reasonable to postulate that the elongate setae of *O. interruptus* function in more of a sensory capacity, to detect water movement, whereas the stout setae of *O. puncticollis* increase crawling efficiency. Careful study of the femoral

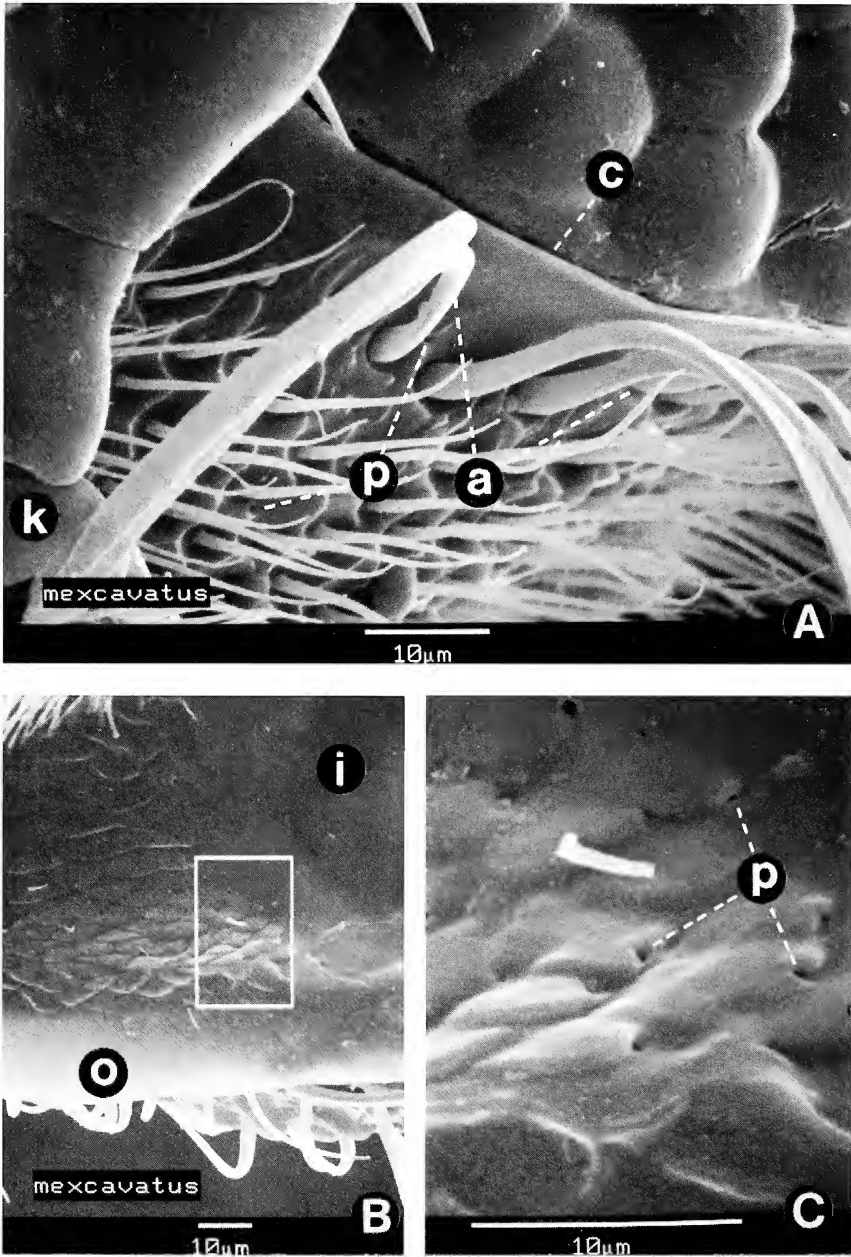


Fig. 4.—*Ochthebius mexcavatus*. A. Psd-sulcus and adjacent area. B. Prothoracic hypomerite, left side. C. Rectangular area in B, enlarged. Structures: (a) psd-setae, (c) psd-sulcus, (i) hypomerite antennal pocket, (k) cupule article of antenna, (o) hh-border, (p) exocrine pores.

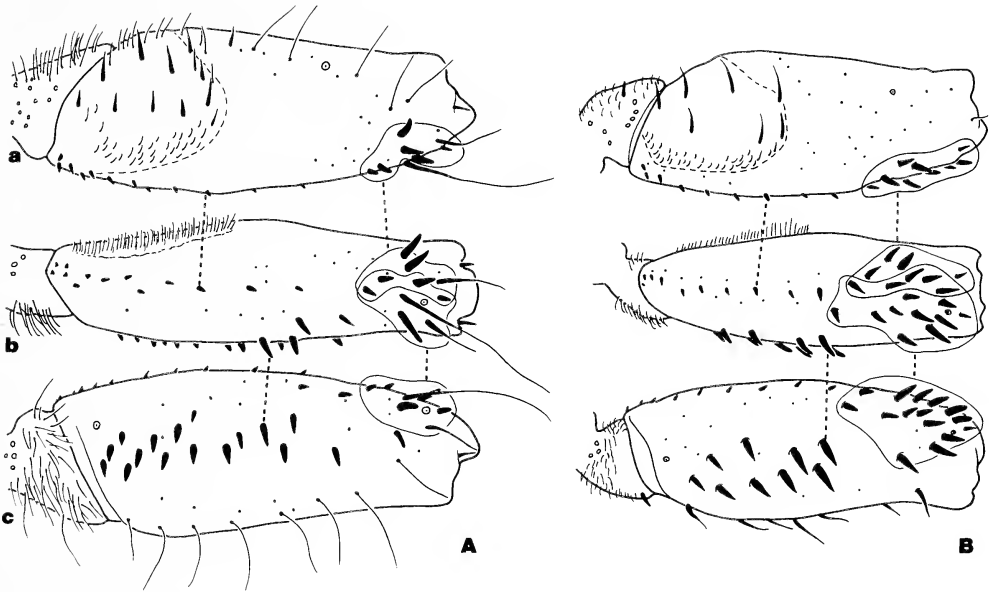


Fig. 5.—Profemur, anterior (a), dorsal (b), and posterior (c) aspects, corresponding setae of distal spine cluster indicated by dashes and loops. A. *Ochthebius interruptus*. B. *O. puncticollis*.

setae of ochthebiines should prove useful for predicting microhabitat preferences of species.

Function of the Hyaline Borders.—The lateral hyaline borders of *Ochthebius* take many shapes and have been important historically in the taxonomy of the genus. However, the hypomer al hyaline border has been overlooked by previous

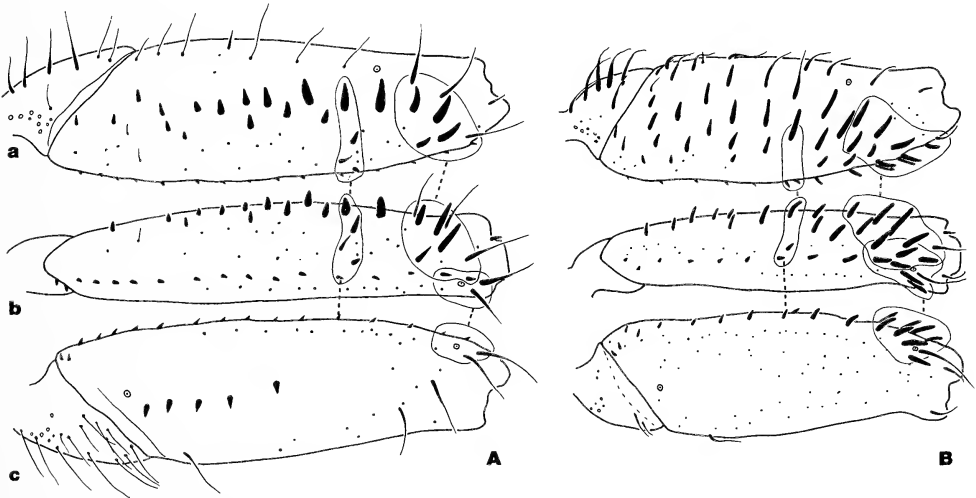


Fig. 6.—Mesofemur, anterior (a), dorsal (b), and posterior (c) aspects, corresponding setae of distal spine cluster indicated by dashes and loops. A. *Ochthebius interruptus*. B. *O. puncticollis*.

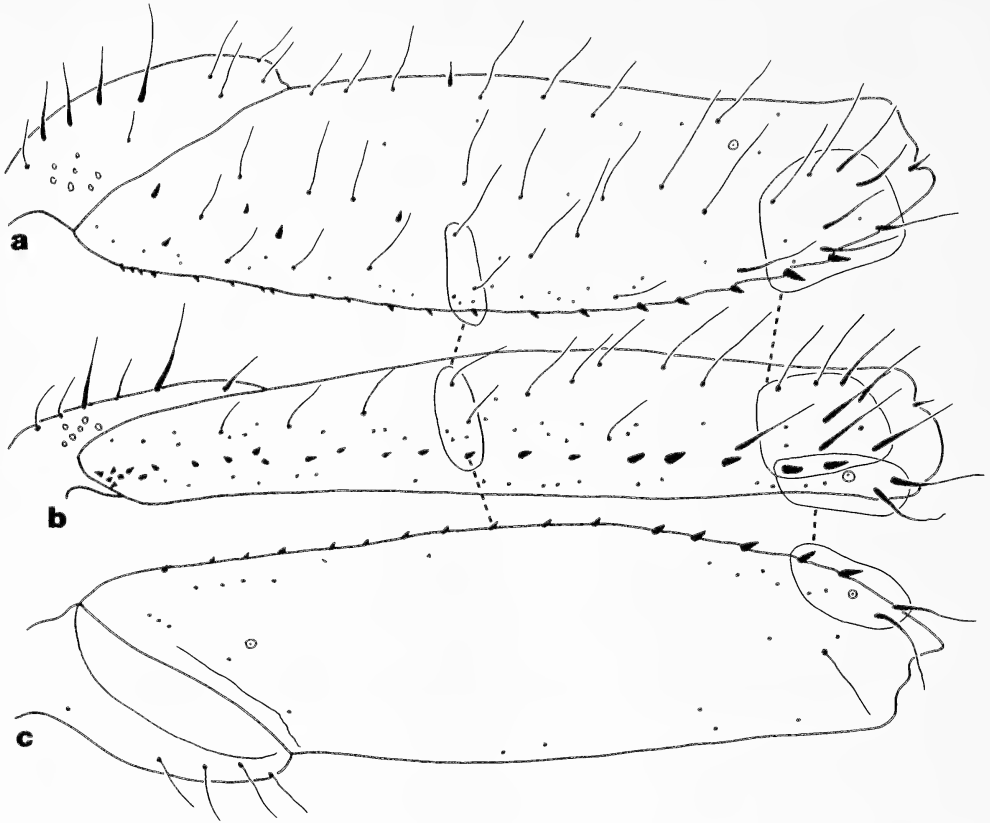


Fig. 7.—*Ochthebius interruptus*, metafemur, anterior (a), dorsal (b), and posterior (c) aspects, corresponding setae indicated by dashes and loops.

workers, and a hypothesis of the function of the hyaline borders has not previously been proposed.

It seems highly likely that the hyaline borders serve as antimicrobial surfaces, and provide spreading surfaces for exocrine gland secretions. The combination of smoothness and flexibility allows the hyaline surfaces to be effectively cleaned of bacteria and debris, and applied with chemicals, while resulting in minimal wear of the surfaces that are rubbed together (the hyaline borders and the scraping setae of the legs), via effective flexibility of the hyaline borders.

The ah- and ph-borders each scrape against opposing, correspondingly smooth surfaces on the head and elytra, respectively. During normal body movements these borders flex and their free margins scrape against the opposing surfaces, preventing bacteria from attaching. The accumulation of bacteria and debris commonly seen on the upper surface of the lh-border is clear evidence of the importance of the hyaline borders to the respiratory system. These hyaline borders may also function in other ways, such as serving as spreading surfaces for pheromones or as evaporative surfaces to aid in the removal of water during grooming.

There seems to be a correspondence between the relative size of the lh-border and the density of the geographical distribution of species. That is, "rare" species with widely disjunct populations often have larger lateral hyaline borders than do

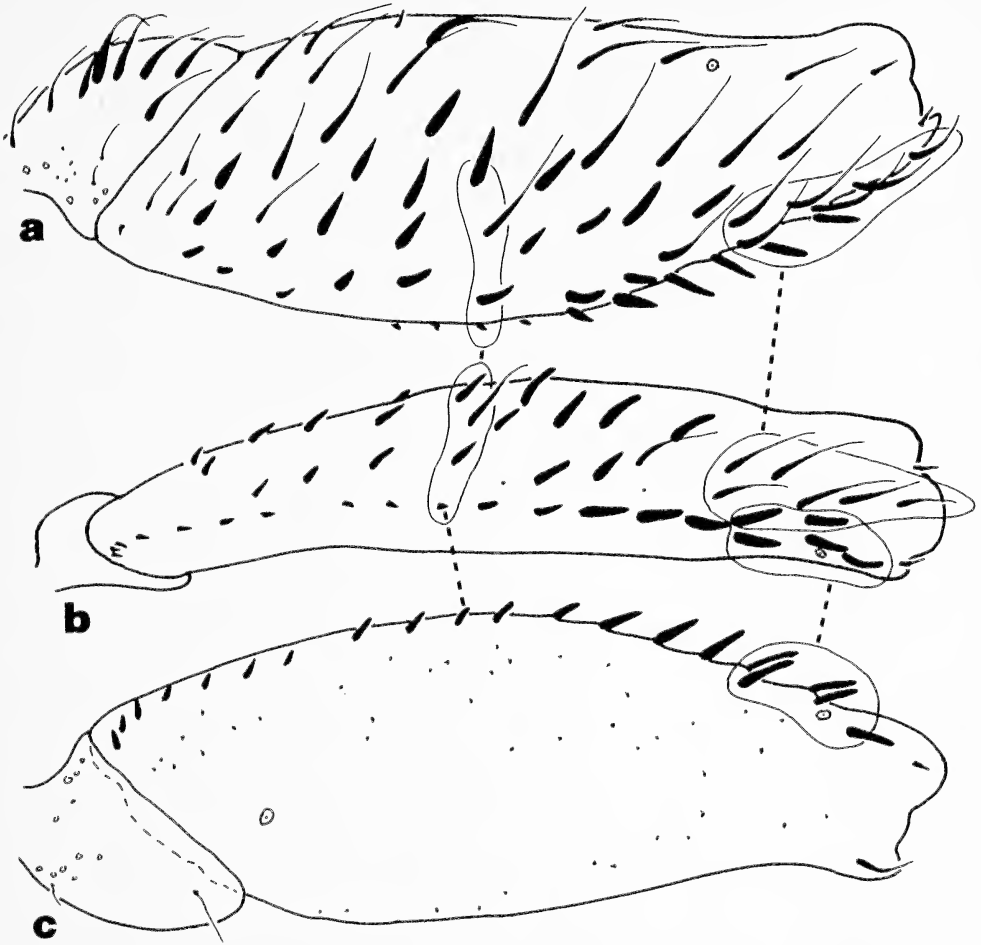


Fig. 8.—*Ochthebius puncticollis*, metafemur, anterior (a), dorsal (b), and posterior (c) aspects, corresponding setae indicated by dashes and loops.

related, more densely populated species. This correspondence needs more study, it may relate to pheromone communication and the evolution of wider hyaline borders.

Derivation of the Hyaline Borders.—Many nonochthebiine Hydraenidae possess an anterior and a posterior hyaline border. This suggests strongly that the ancestral ochthebiine had these structures.

The new genus *Protochthebius* (see description below) has the presumed ancestral condition. A hyaline border is located ventrally at the lateral margin of the hypomeron. Since this hyaline border forms the bubble margin, it is interpreted as being the hh-border, although it is located almost laterally. Unlike the derived hh-border of *Ochthebius*, which is in a vertical plane, the hh-border of *Protochthebius* is oriented in a more horizontal plane and is therefore visible in dorsal aspect, extending slightly beyond the lateral margin of the pronotum. The post-ocular area lacks both the psd-sulcus and the psd-setae, and the hypomeral an-

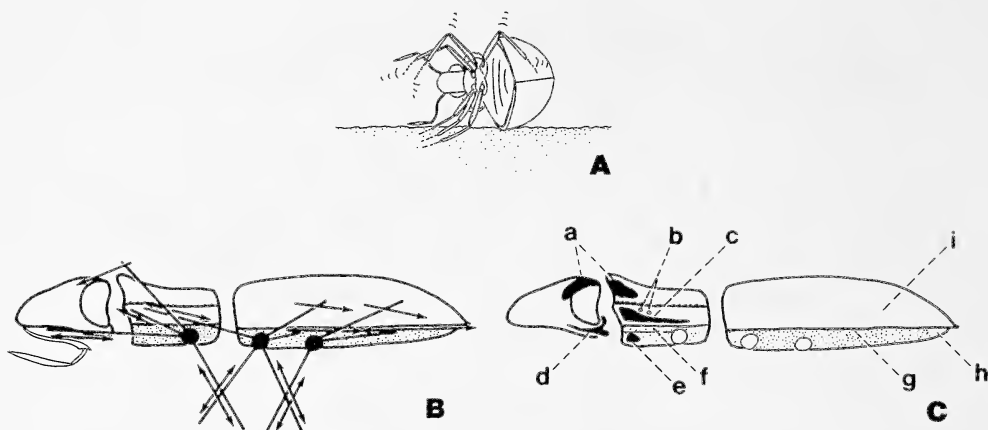


Fig. 9.—*Hydraena americana*, schematic. A. Beetle balanced on edge, the tibiae of the right legs resting on the surface of a wet leaf, the left legs performing secretion-grooming. B. Secretion-grooming movements of left tibiae (note pivotal role of middle leg). C. Locations of exocrine gland pore areas (PA) and sensillar areas (SA): (a) pronotal SA on anterolateral angle, (b) hypomeral dome-shaped sensillar pair, (c) hypomeral PA, (d) postocular and genal PA/SA, (e) prosternal PA, (f) hypomeral exocrine sulcus (PA) for maintaining respiratory bubble, (g) elytral epipleuron (PA), (h) apical abdominal sterna, outside of respiratory bubble (PA), (i) elytral exocrine glands (associated with serial punctures and setae).

tennal pocket setae are absent. The antennal pocket is extremely shallow and entirely pubescent.

The hh-border extends the full length of the hypomeron in the vast majority of species of *Ochthebius*. Only extremely rarely is the posterior part of the hh-border lost without a trace. This loss appears to be associated with the development of extremely wide lh-borders. An example of this is *O. spatulus* (Fig. 32C).

Only very rarely does the prothorax lack the lh-border, while having the other three (for example, an undescribed species from Nepal). Additional study is needed to determine if this indeed represents a primary condition, or results from a secondary loss of the lh-border.

Genus *Hydraena*

Secretion-Grooming Behavior.—The secretion-grooming behavior of *Hydraena* described below is based on observations of two closely related and very morphologically similar North American species, *H. americana* and *H. vandykei*.

Although the cosmopolitan genus *Hydraena* is quite diverse in body form and dorsal sculpture, the ventral structures involved in secretion-grooming do not show marked differences. Therefore, the behavior described below might reasonably be anticipated in many other (if not all) species of the genus. It remains to be determined whether the modified male protibiae and metatibiae found in many species of the genus relate in some way to differences in secretion-grooming behavior; the two species reported on here do not have sexually dimorphic legs.

At the outset of secretion-grooming, which is performed out of the water, the beetle positions the legs on one side such that the tibiae are resting on a wet surface (such as a partially decomposed leaf). The body is then tilted until the legs on the opposite side are in the air, the body therefore being “on edge” (Fig. 9A).

The “free” legs then begin a process of repeatedly rubbing certain areas of the cuticle with the tibiae (Fig. 9B). As the secretion-grooming progresses, the legs and the parts of the body rubbed by the legs take on a glistening appearance, presumably due to a coating of the exocrine secretions.

Several of these rubbing actions, especially the remarkable placement of the mesotibia against the hypomerion, are accomplished with the prothorax rotated and angled relative to the pterothorax. This positioning is possible because of the wide intersegmental membrane between the pro- and mesothorax. Located in this membrane are the mesothoracic spiracles; rotation of the prothorax opens this area and exposes the surfaces.

The protibia principally rubs four locations: (1) the anterior part of the bubble-hypomerion, rubbing back and forth along the anterior part of the hypomeral secretion delivery surface and hsd-sulcus (e.g., Fig. 9C:f, 12); (2) the anterior part of the wet-hypomerion, rubbing back and forth in the general area where are located three separate clusters of exocrine pores (Fig. 9C:c, 11B:i, 14B:i); (3) the undersurface of the head, rubbing back and forth, from the genal antennal pocket setae, along the antennal groove beneath the eye, and forward to the lateral process of the mandible (Fig. 9C:d, 20A:b); and (4) the dorsal part of the anterolateral angle of the pronotum, in a sweeping motion forward, first over the anterolateral elongate setae, and then over the top of the eye (Fig. 9C:a).

The mesotibia is extremely interactive, having principally four operations: (1) stroking backward on the elytron, sometimes in unison with the metatibia; (2) mutual rubbing back and forth with the metatibia; (3) similar rubbing with the protibia; and (4) rubbing back and forth on the hypomerion (inserted between the body and the profemur), sometimes stroking the hypomerion in unison with the protibia.

The mesotibia plays a pivotal role in mixing and distributing the glandular secretions, in addition to removing debris and microorganisms. The actions of the middle legs are remarkable for their dexterity and rapidity. Often the mesotibia alternately rubs the protibia and the metatibia; that is, while the protibia is performing its grooming actions on the head and prothorax, the meso- and metatibia are rubbing each other, then the meso- and protibia start mutual rubbing and the metatibia returns to rubbing the elytra. Sometimes the mesotibia, in sequence, rubs the hypomerion, then the protibia, then the metatibia. The mesotibia also rubs all surfaces of the profemur and metafemur. The metatibia repeatedly strokes the side and edge of the elytron, and sometimes strokes the apical abdominal sterna.

Other tibial rubbing observed in specimens in a typical standing position include pro- and mesotibial mutual rubbing, and rubbing of the metatibiae against each other and against the apical sterna.

ESDS Cuticular Components.—In contrast to the ESDS of *Ochthebius*, in *Hydraena* the concentration of exocrine glands associated with the bubble margin are located in the prothorax. Although the postocular area of *Hydraena* is complex (see below), there is no exocrine gland system similar to that of *Ochthebius*. The antennal pocket is formed differently than that of *Ochthebius*, and contains an antennal cleaner, a structure not present in *Ochthebius*.

Hypomeral Secretion Delivery Sulcus.—The pores of exocrine glands associated with the bubble margin lie in a longitudinal groove, the hypomeral secretion delivery (hsd-) sulcus (g in Fig. 10B; 12A, B; and 14A). The hsd-sulcus is extremely narrow, and in some groups is not visible (even with SEM) unless the specimen is treated with potassium hydroxide (to remove the smooth secretion

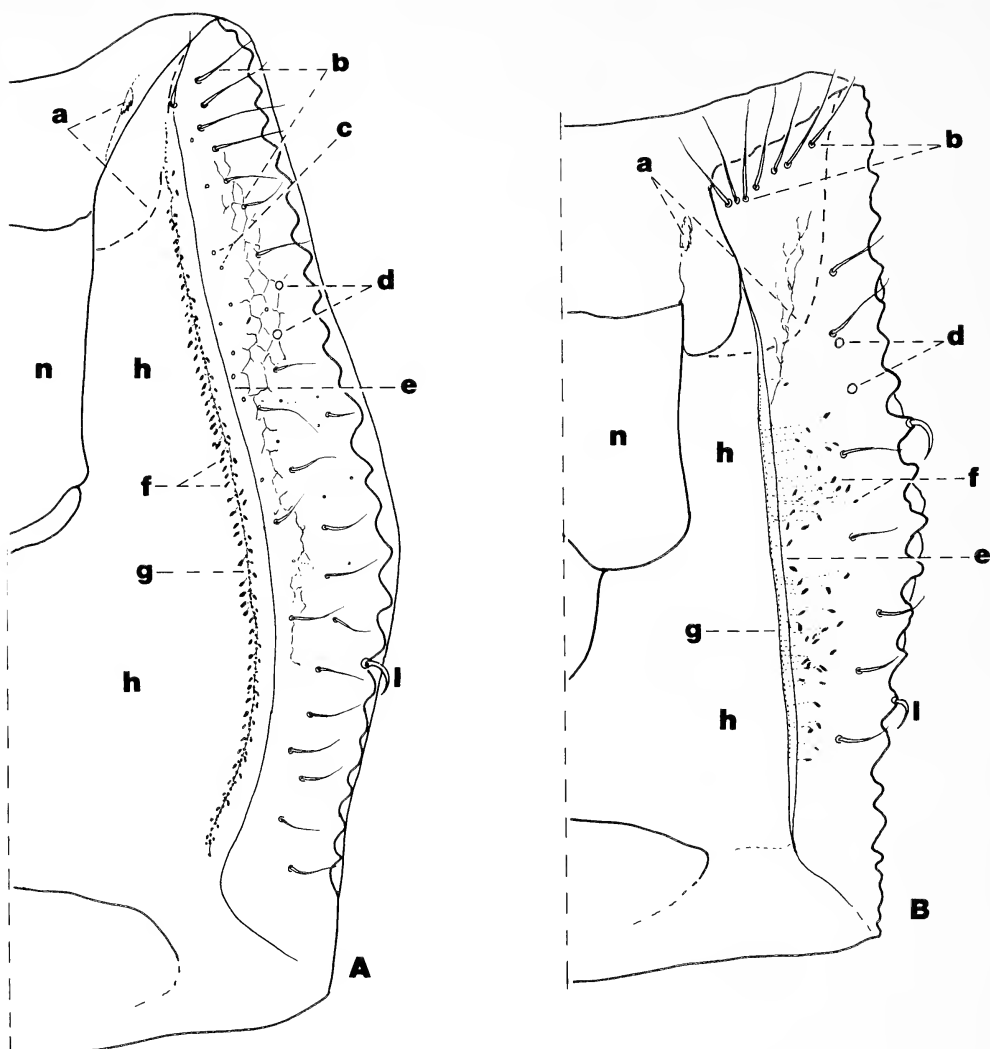


Fig. 10.—*Hydraena*, venter of left side of prothorax. A. *H. gracilis*. B. *H. testacea*. Structures: (a) antennal cleaner and antennal pocket, (b) hap-setae, (c) exocrine pores of wet-hypomeron, (d) hypomeral dome-shaped sensillar pair, (e) hsd-carina, (f) end-apparatus and ductules of exocrine glands, (g) hsd-sulcus on hsd-surface, (h) hydrofuge hypomeron, (l) lateral seta, (n) prosternum.

filling the sulcus). It is possible that, in some groups, part of the sulcus is closed, forming a tube that delivers the secretion toward the antennal pocket (see Fig. 13B); incisive histological study is needed to clarify this.

The hsd-sulcus is located on a relatively smooth and raised surface, the hypomeral secretion delivery (hsd-) surface. In the subgenus *Haenydra* (e.g., *gracilis*) the hsd-surface (Fig. 13A:g, 14A:g) is flat, completely smooth, and equally wide on both sides of the hsd-sulcus. In other groups (e.g., the nominate subgenus) the hsd-surface is slightly convex, and the hsd-sulcus lies along the medial margin of this ridge, the hsd-surface between the hydrofuge area and the hsd-sulcus being comparatively narrow (e.g., *riparia*; Fig. 12A, B). In still other groups (e.g., the

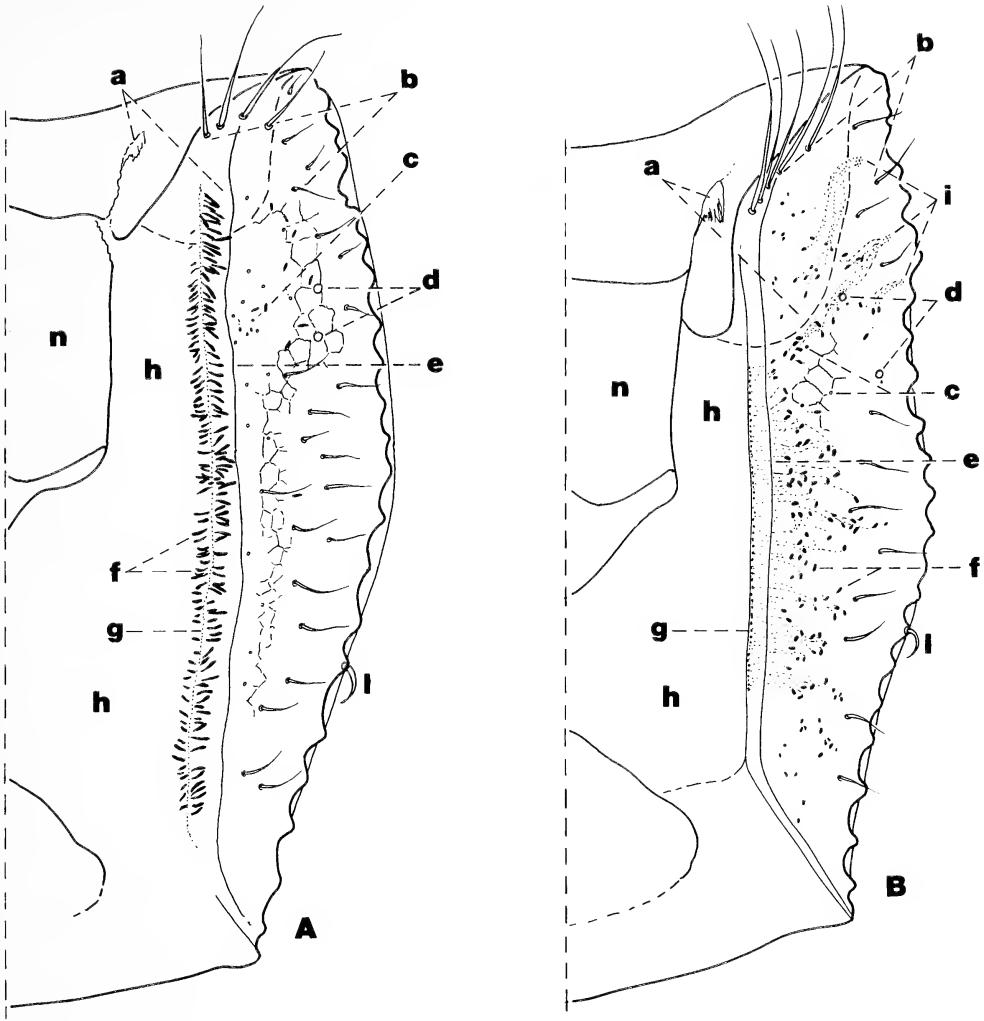


Fig. 11.—*Hydraena*, venter of left side of prothorax. A. *H. riparia*. B. *H. americana*. Structures: (a) antennifer and antennifer pocket, (b) hap-setae, (c) exocrine pores of wet-hypomeron, (d) hypomeral dome-shaped sensillar pair, (e) hsd-carina, (f) end-apparatus and ductules of exocrine glands, (g) hsd-sulcus on hsd-surface, (h) hydrofuge hypomeron, (i) exocrine pore clusters of wet-hypomeron, (l) lateral seta, (n) prosternum.

subgenus *Phothydraena*) the hydrofuge surface is contiguous with the hsd-sulcus, the latter lying along the medial margin of the quite convex (nearly cariniform) hsd-surface (e.g., *testacea*; Fig. 18A:g). The hsd-surface terminates laterally in the hypomeral secretion delivery (hsd-) carina, a sharp cuticular ridge that forms the lateral boundary of the bubble-hypomeron.

Antennal Pocket and Antennal Cleaner.—The antennal pocket is well formed and has, at its anteromedian extreme, a well-defined cluster of specialized spines that is here interpreted, based on location and shape, to be an antennal cleaning device. The antennal cleaner varies among the species groups in the degree of clustering of the spines. For example, the spines are densely clustered in *Hydraena*

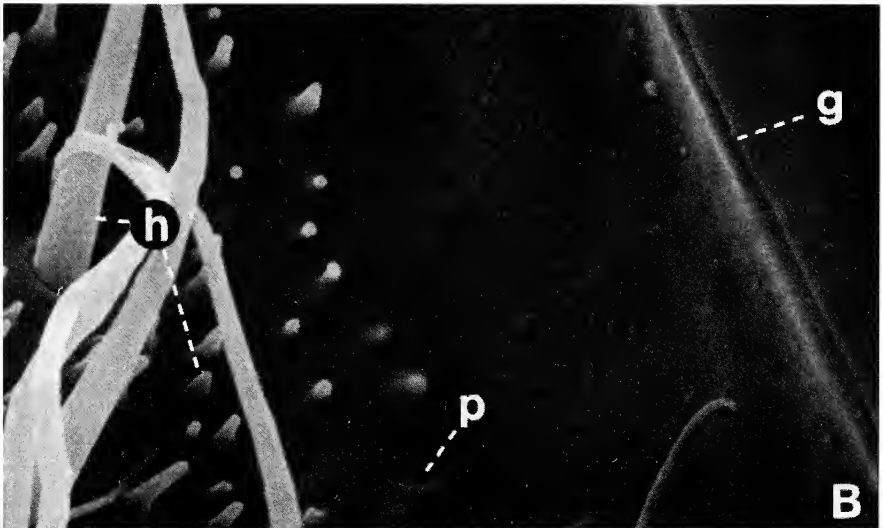
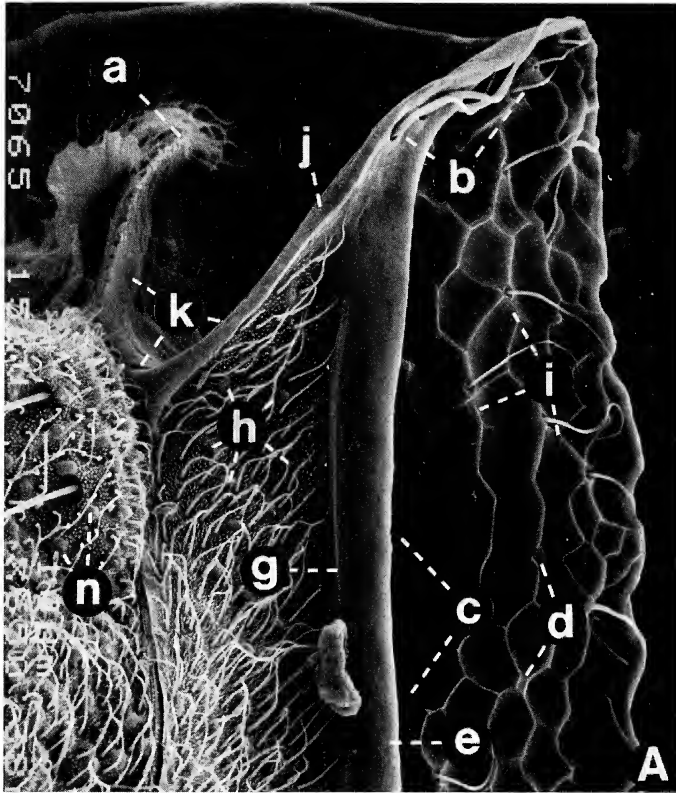


Fig. 12.—*Hydraena riparia*. A. Hypomeron, anterior aspect of left side. B. Detail of exocrine sulcus (g) and adjacent hydrofuge. Structures: (a) antennal cleaner, (b) hap-setae, (c) exocrine pores of wet-hypomeron, (d) hypomeral dome-shaped sensillar pair, (e) hsd-carina, (g) hsd-sulcus on hsd-surface, (h) asperite hydrofuge hypomeron and (in A) secretions, (i) exocrine pore clusters of wet-hypomeron, (j) marginal asperites of antennal pocket, (k) marginal pores of antennal pocket, (n) prosternum, (p) exocrine pore of hydrofuge hypomeron.

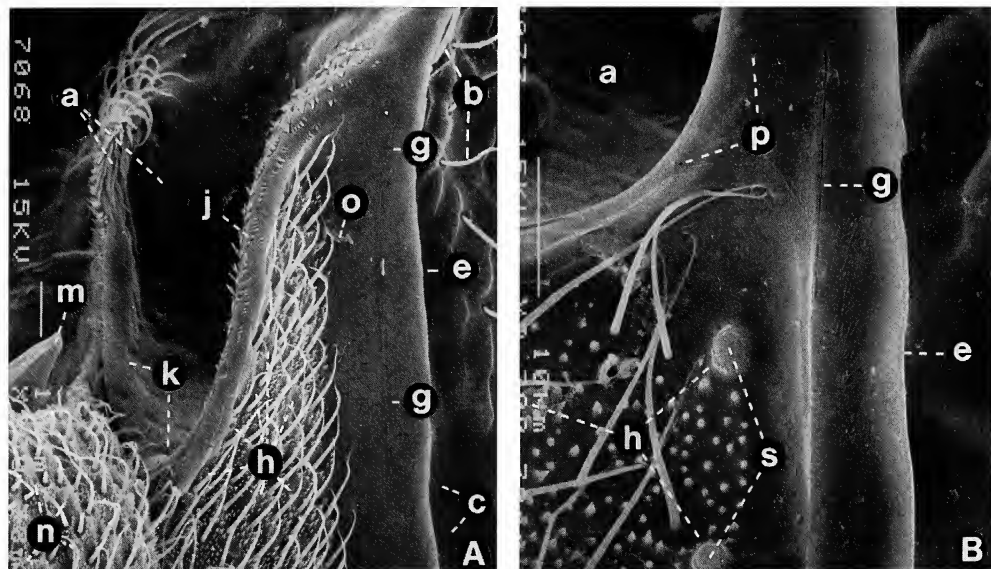


Fig. 13.—*Hydraena*, hypomeron and antennal pocket. A. *H. gracilis*, anterior aspect of left side. B. *H. americana*, detail of exocrine sulcus (g) and adjacent asperite hydrofuge. Structures: (a) antennal cleaner and antennal pocket, (b) hap-setae, (c) exocrine pores of wet-hypomeron, (e) hsd-carina, (g) hsd-sulcus on hsd-surface, (h) exocrine pores in asperite hydrofuge hypomeron, (j) marginal asperites of antennal pocket, (k) marginal pores of antennal pocket, (m) cervical sclerite, (n) prosternum, (o) bacteria, (p) marginal pores of antennal pocket, (s) secretion “caps” of exocrine pores.

“new species A” (Fig. 15B, 16D) and *H. americana* (Fig. 17A, B), but less densely clustered in *H. testacea* (Fig. 16A, B), *H. riparia* (Fig. 16C), and *H. gracilis* (Fig. 17C, D).

Associated with the antennal cleaner is a bottle-shaped sensillum, located more toward the “head side” of the antennal cleaner (Fig. 15B:s; 16:b; 17:b), asperite hydrofuge pubescence (e.g., Fig. 16A:h), and exocrine pores of the antennal pocket (e.g., Fig. 16A:p). The antennal pocket has exocrine pores near the posterior margin (k in Fig. 12, 13, and 18), and often has sharp, tiny asperites on its lateral margin (j in Fig. 12 and 13).

Hypomeral Hydrofuge.—The bubble-hypomeron posterior to the antennal pocket is clothed in asperite hydrofuge consisting of flagelliform setae and much smaller, denser asperites (the prosternum has similar asperite hydrofuge). The shapes, sizes, and density of the flagelliform setae and (especially) the asperites vary among the species groups (h in Fig. 12–14).

Interspersed in the asperite hydrofuge are single exocrine pores. In many groups each pore is surrounded by tiny asperites to form an exocrine pore crown (h in Fig. 13B and 18C, D). In some SEM preparations, a secretion cap can be seen covering the pore crown (s in Fig. 13B and 18C [cap dislodged from its crown]).

Structures of the Wet-hypomeron.—Hypomeral antennal pocket (hap-) setae, usually seven in number, are located near the margin of the antennal pocket (b in Fig. 10–13 and 18; Fig. 19:m). (These setae are not homologous with the hap-setae of *Ochthebius*.) The locations of the hap-setae vary among the species groups.

In all species studied, hypomeral paired (hp-) sensilla (d in Fig. 10–12 and 18)

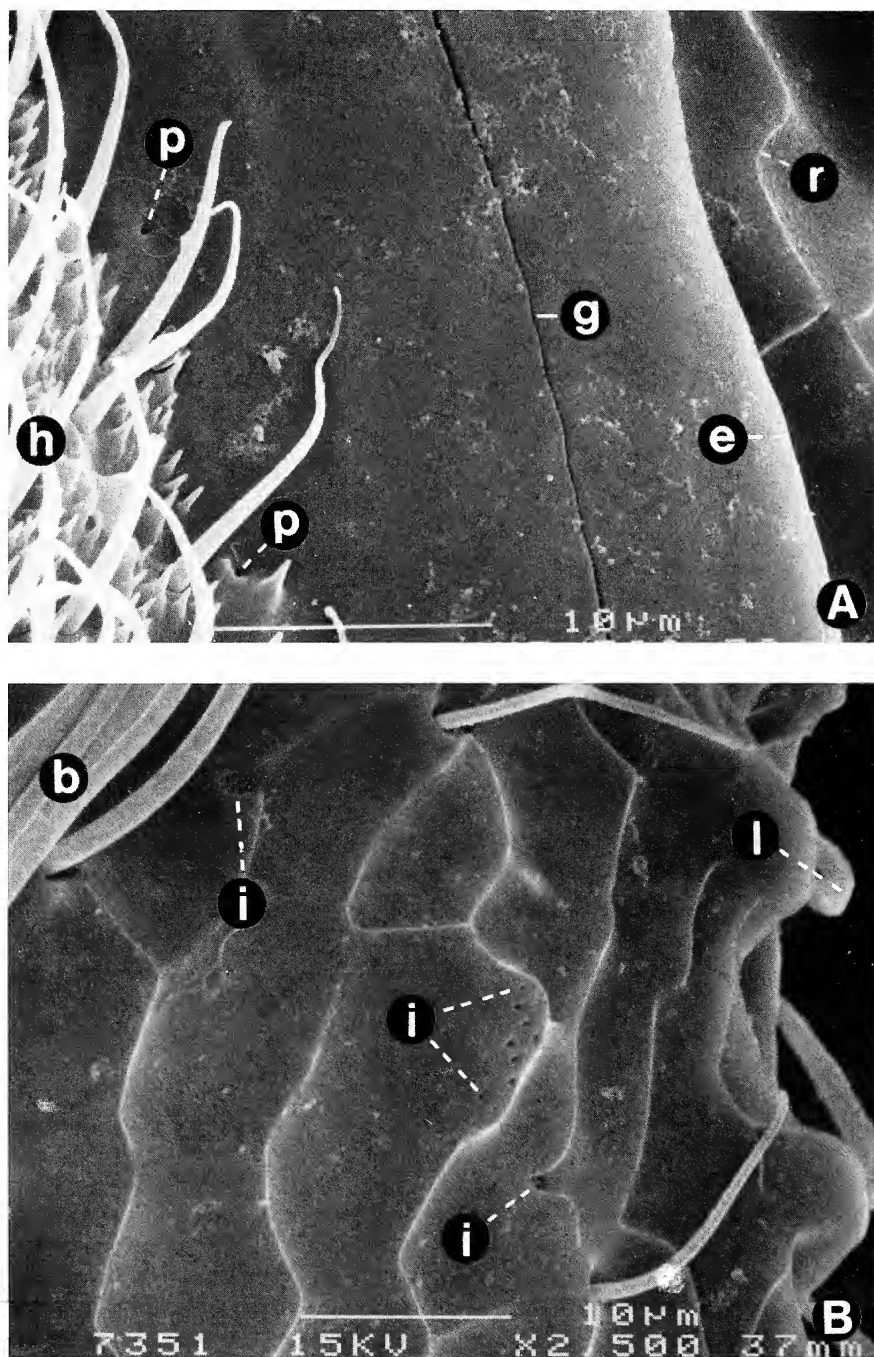


Fig. 14.—*Hydraena*, hypomeron, left side. A. *H. gracilis*, exocrine sulcus (g) and adjacent asperite hydrofuge. B. *H. americana*, anterior aspect of wet-hypomeron. Structures: (b) hap-setae, (e) hsd-carina, (g) hsd-sulcus on hsd-surface, (h) asperite hydrofuge, (i) exocrine pore clusters of wet-hypomeron, (l) lateral seta, (p) exocrine pores in asperite hydrofuge hypomeron, (r) microreticulation.

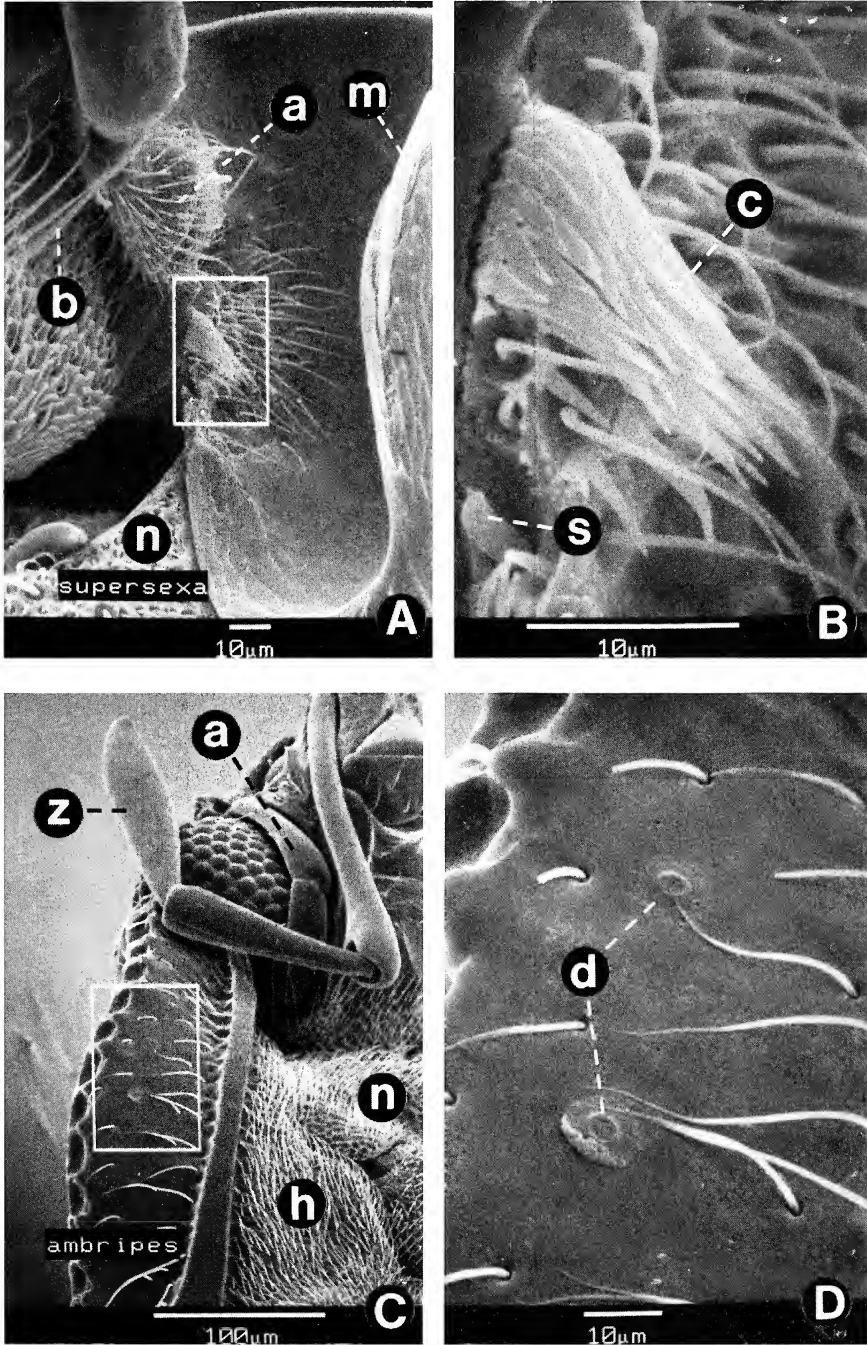


Fig. 15.—*Hydraena* (undescribed species from Papua New Guinea). A. Species "S," postocular area and antennal pocket. B. Rectangular area of A, enlarged. C. Species "A," hypomeron, right side. D. Rectangular area of C, enlarged. Structures: (a) antenna, (b) gap-setae, (c) antennal cleaner, (d) dome sensillar pair of wet-hypomeron, (h) hydrofuge hypomeron, (m) antennal pocket setae, (n) prosternum, (s) bottle-shaped sensillum, (z) maxillary palpus.

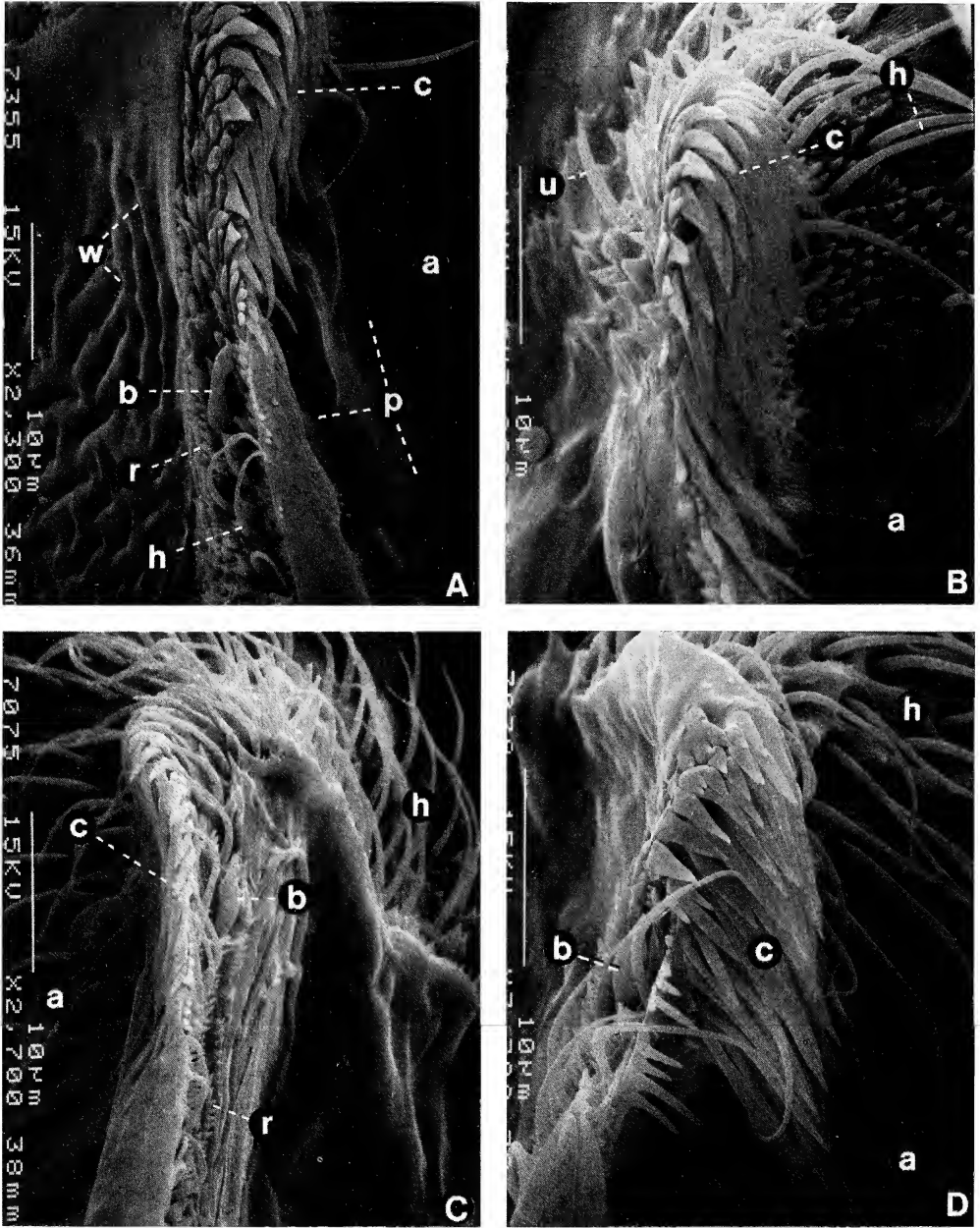


Fig 16.—*Hydrogna*, antennal cleaners. A, B. *H. testacea*. C. *H. riparia*. D. Undescribed species "S," Papua New Guinea. Structures: (a) antennal pocket, (b) bottle-shaped sensillum, (c) antennal cleaner, (h) asperite hydrofuge pubescence, (p) exocrine pores of antennal pocket, (r) asperites of antennal pocket margin, (u) sensillum(?), (w) cuticular wrinkles.

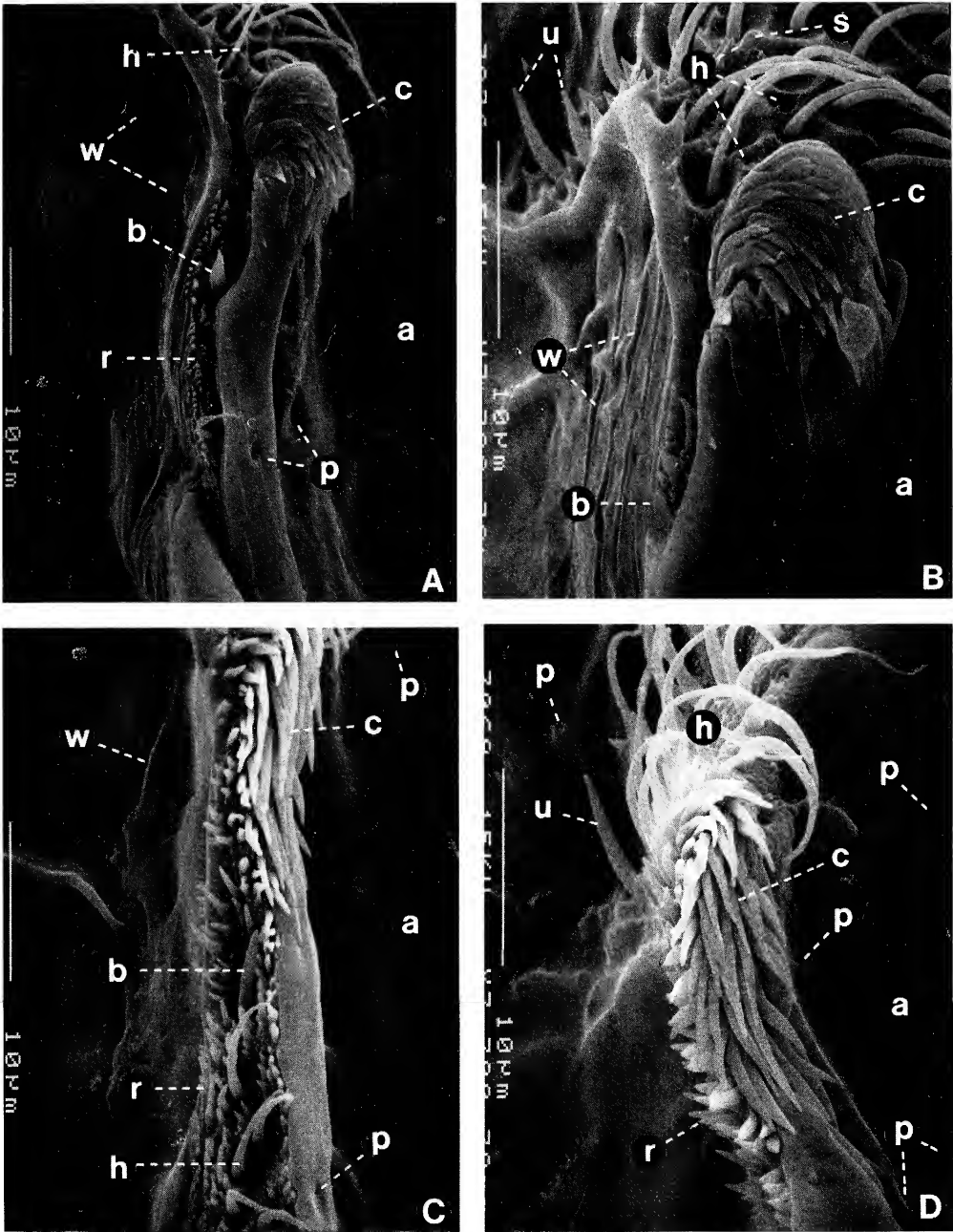


Fig. 17. *Hydraena*, antennal cleaners. A, B. *H. americana*. C, D. *H. gracilis*. Structures: (a) antennal pocket, (b) bottle-shaped sensillum, (c) antennal cleaner, (h) asperite hydrofuge pubescence (exocrine pores indicated in A and B, (p) exocrine pores of antennal pocket, (r) asperites of antennal pocket margin, (s) secretion "cap" on exocrine pore in hydrofuge area, (u) sensilla(?), (w) cuticular wrinkles.

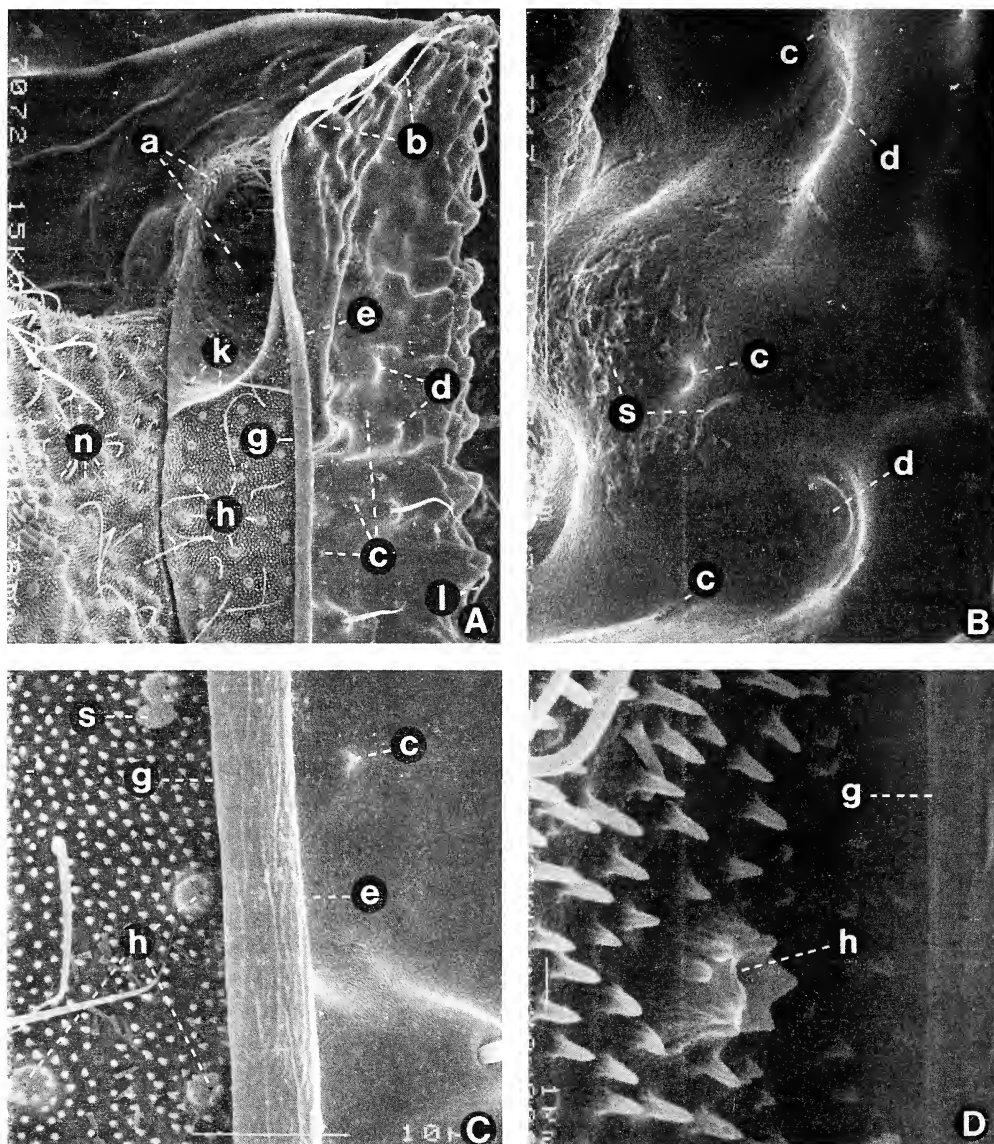


Fig. 18.—*Hydraena testacea*, hypomeron. A. Anterior aspect of left side. B. Detail of dome-sensilla. C. Detail of hypomeran carina and adjacent structures. D. Detail of exocrine sulcus. Structures: (a) antennal cleaner and antennal pocket, (b) hap-setae, (c) exocrine pores of wet-hypomeron, (d) hypomeran dome-shaped sensillar pair, (e) hsd-carina, (g) hsd-sulcus on hsd-surface, (h) exocrine pore "crowns" of asperite hydrofuge hypomeron, (k) marginal pores of antennal pocket, (l) lateral seta, (n) exocrine pore "crowns" of prosternum, (s) presumed exocrine secretion.

are located in the anterior half of the wet-hypomeron, approximately opposite the prosternum. These structures are tiny pits with a thin cuticular cover having a minute central pore (Fig. 18B:D). Histological study will probably show the hp-sensilla to be chemoreceptive coeloconic sensilla (consisting of a sensory peg

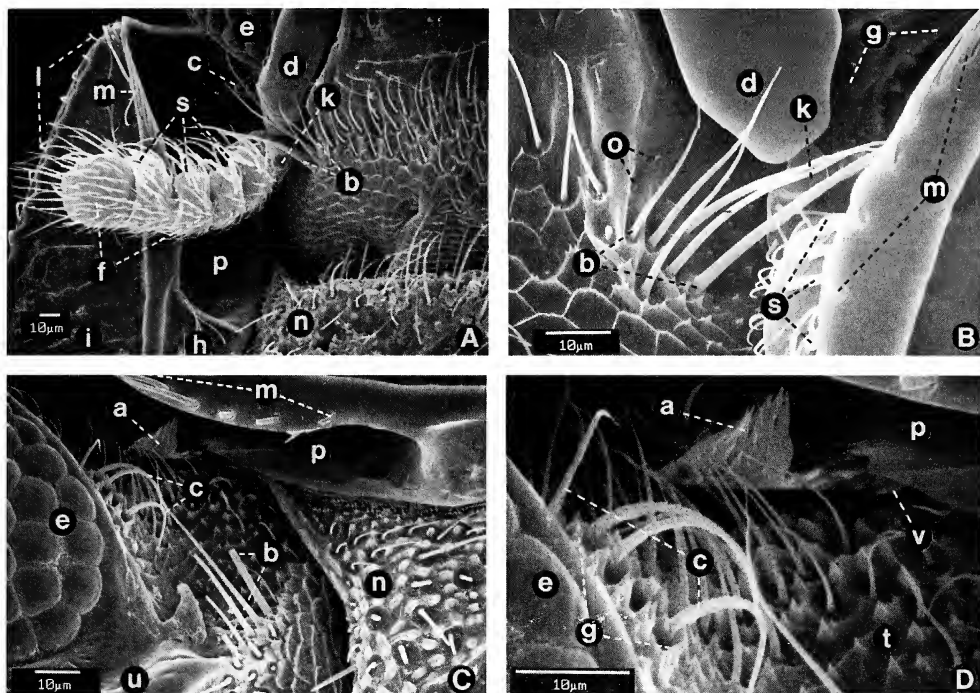


Fig. 19.—*Hydraena* (undescribed species from Papua New Guinea), postocular area and antennal pocket. A. Species "THO," right side, antennal club. B. Species "R.," left side, gena and antenna. C, D. Species "Q.," left side. Structures: (a) antennal cleaner, (b) gap-setae, (c) postocular setae, (d) second antennomere, (e) eye, (f) antennal hydrofuge pubescence, (g) postocular peg sensilla, (h) hydrofuge hypomeron, (i) wet-hypomeron, (k) cupule article of antenna, (l) lateral setae, (m) antennal pocket setae, (n) prosternum, (o) exocrine pores, (p) antennal pocket, (s) sensilla of antennal club, (t) genal asperite hydrofuge, (u) subocular antennal groove, (v) bottle-shaped sensillum.

in a fluid-filled cavity). In one SEM preparation (Fig. 15D:d), the hp-sensilla are covered with a secretion residue.

Single exocrine pores (c in Fig. 10A and 11A, B) are located on the wet-hypomeron, often more closely spaced together (but not clustered) on the area medial to the pair of chemosensilla. In some species, exocrine pore clusters (Fig. 11B:i, 14B:i) are located in the anterior part of the wet-hypomeron.

Sub- and Postocular Antennal Grooves.—In repose, the antenna is held beneath and behind the eye. The first two antennomeres are held beneath the eye, in the subocular antennal (sa-) groove. The sa-groove is usually weakly sculptured (e.g., Fig. 20A; 21A, C).

The postocular and genal areas are separated by the postocular antennal (pa-) groove (Fig. 20:a, 21:a), which is continuous with the sa-groove. The pa-groove is smooth or at most very finely microreticulate, in contrast to the strongly sculptured and setose areas it separates.

When the antenna is held in repose, the antennomeres in contact with the smooth pa-groove are the second (its distal part), the third (a tiny intermediate article), the fourth (the cupule), and perhaps the basal part of the fifth (the first article of the pubescent club; Fig. 19A, B). Therefore, these articles are in a position such that, when the antenna is raised during air capture, the articles would

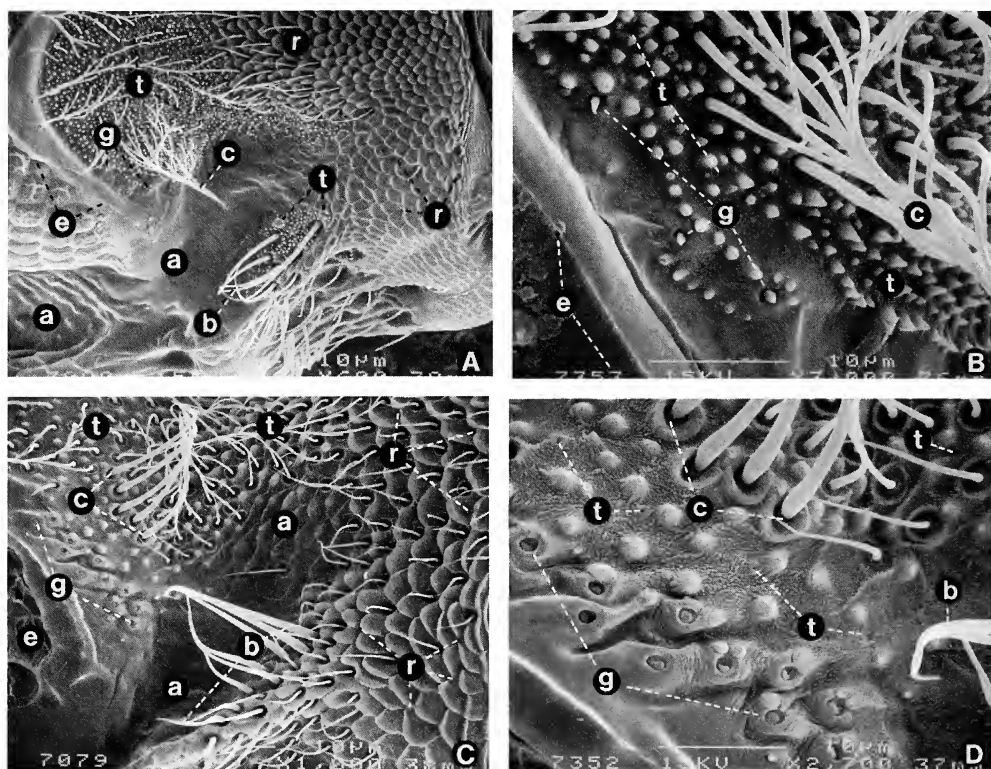


Fig. 20.—*Hydraena*, sub- and postocular areas. A. *H. testacea*. B. Same, detail of peg sensilla area. C. Undescribed species "S" (Papua New Guinea). D. Same, detail of peg sensilla area. Structures: (a) sub- and postocular antennal groove, (b) gap-setae, (c) postocular sensory setae, (e) eye and periocular exocrine pores, (g) postocular peg sensilla, (r) exocrine pores of reticulate hydrofuge, (t) exocrine pores of asperite hydrofuge.

stroke against (or at least nearly touch) the sensilla and setae at the posteroventral angle of the eye.

Because of the flexibility of the antenna at the cupule, the other articles of the pubescent club (articles 6–9) may also be able to stroke against the postocular sensilla and setae when the antenna is raised during air capture.

Postocular Structures.—Six kinds of cuticular microstructures are located in the postocular area: peg sensilla, grooved sensilla, asperites, asperite hydrofuge, reticulate hydrofuge, and exocrine pores.

Peg sensilla (Fig. 19D:g, 20:g) are located adjacent to the orbit of the eye (behind the posteroventral angle of the eye). The amount and density of the peg sensilla, and particulars of the cuticular topography surrounding them, vary among the species groups.

Grooved sensilla (c in Fig. 19, 20, 21D) form a distinct cluster slightly separated from the peg sensilla. These setae are almost certainly chemoreceptors—fractured sensilla appear to have a central lumen (Fig. 21B). These sensilla appear to be articulated at their bases (i.e., sensilla chaetica), although varying from tightly articulated in some groups (Fig. 20B; 21B, D) to having a wide cup-like base indicating a wide range of setal motion (Fig. 20C, D:c).

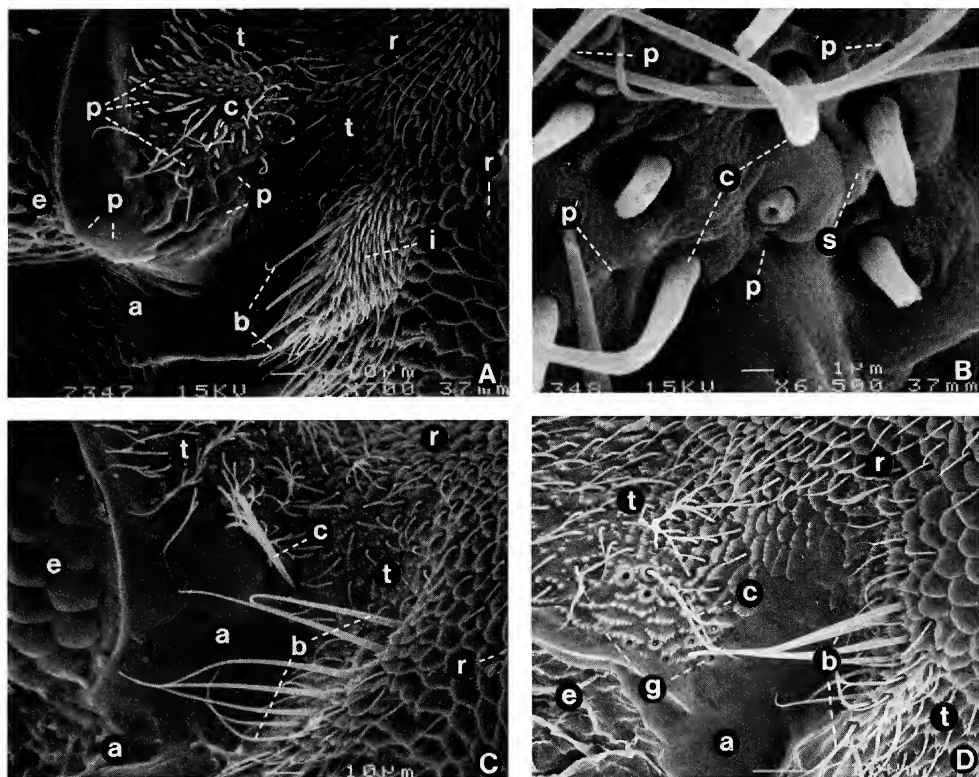


Fig. 21.—*Hydraena*, sub- and postocular areas. A. *H. gracilis*. B. Same, detail of postocular grooved sensory setae. C. *H. riparia*. D. Undescribed species "THU" (Papua New Guinea). Structures: (a) sub- and postocular antennal groove, (b) gap-setae, (c) postocular sensory setae (grooved in B), (e) eye, (g) postocular peg sensilla, (i) genal spiculate area, (p) exocrine pores, (r) reticulate hydrofuge (peg sensillum in A and C), (s) presumed exocrine secretion, (t) asperite hydrofuge.

Asperites, tiny cone-shaped tubercles (Fig. 20:t), are present between and among the peg sensilla and grooved sensilla. In some species the asperites form short linear groups (e.g., Fig. 21D).

In all species, at least part of the postocular area has hydrofuge hairs, varying in density depending upon the species group. In some species the ground microsculpture of the hydrofuge area consists of asperites, forming asperite hydrofuge (e.g., Fig. 20:t). Alternatively, the ground sculpture can consist of microreticulation, forming reticulate hydrofuge (e.g., Fig. 20:r). Exocrine pores (unclustered) are located in various parts of the postocular area (Fig. 20:t, 21B:p).

Genal Structures.—A cluster of long, stiff, tapering setae, the genal antennal pocket (gap-) setae (b in Fig. 19, 20, and 21), are positioned such that, when the antenna is in repose, the gap-setae cover and protect the third, fourth (cupule), and distal portion of the second antennomere. These pivotal antennomeres are the smallest, and presumably the most susceptible to breakage. The cuticular ground sculpture at the gap-setae is asperite, varying from weakly (Fig. 20A), to moderately strongly (Fig. 19B; 20C; 21C, D), to very strongly developed (spiniform; Fig. 21A).

The gap-setae and spiniform asperites probably act as combs that, in addition

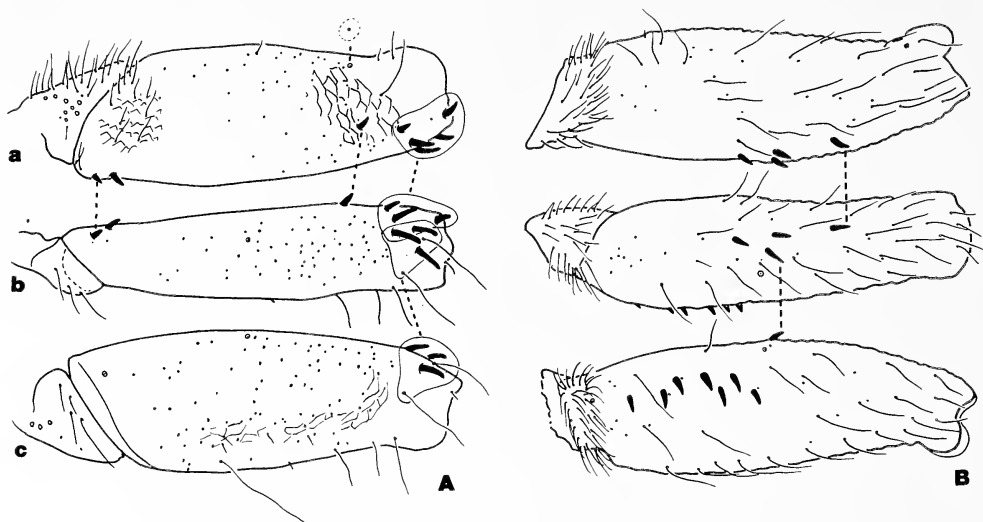


Fig. 22.—Profemur, anterior (a), dorsal (b), and posterior (c) aspects, corresponding setae of distal spine cluster indicated by dashes and loops. A. *Limnebius piceus*. B. *Hydraena americana*.

to the antennal cleaner of the prothorax, clean the pubescent antennal club as it moves in and out of the antennal pocket. Reticulate hydrofuge or asperite hydrofuge is located medial to the gap-setae (Fig. 19A). In some preparations, exocrine pores are visible near bases of the gap-setae (e.g., Fig. 19B:o).

Femoral Setae.—The femora of *H. americana* (Fig. 22B, 23B, 24B) bear many elongate and flexible setae, and few short, stout setae. The locations of the stout setae, on the “facing” surfaces of the pro- and mesofemora, correspond with the mutual rubbing that occurs during secretion grooming.

The lack of distal spine clusters on the femora (see *Ochthebius*) reflects the

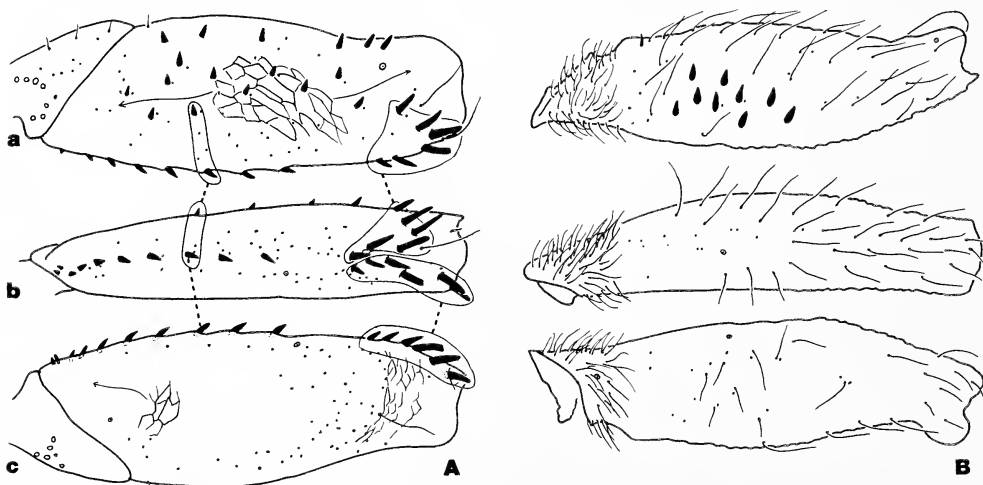


Fig. 23.—Mesofemur, anterior (a), dorsal (b), and posterior (c) aspects, corresponding setae of distal spine cluster indicated by dashes and loops. A. *Limnebius piceus*. B. *Hydraena americana*.

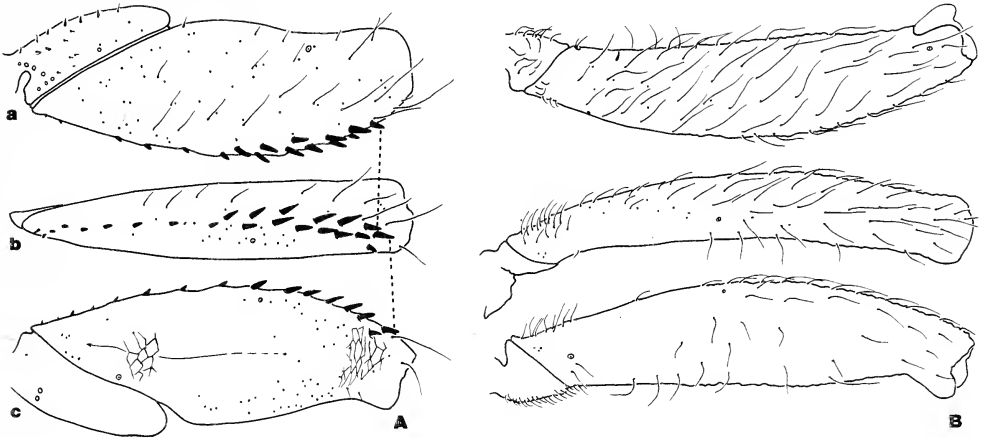


Fig. 24.—Metafemur, anterior (a), dorsal (b), and posterior (c) aspects, corresponding setae indicated by dashes. A. *Limnebius piceus*. B. *Hydraena americana*.

fact that during secretion-grooming it is the tibiae, not the distal part of the femora, that rub other body parts.

Genus *Limnebius*

Secretion-grooming Behavior.—The secretion-grooming behavior of *Limnebius* described below is based on observations of *L. piceus*, a species from western North America. Aspects of the habitat preferences of the genus and the taxonomy of this species are given by Perkins (1976, 1981).

Although nearly cosmopolitan in distribution, with many species, the genus *Limnebius* is extremely uniform in morphology. I have examined representatives of several species, including some near the size extremes (i.e., the largest and smallest) and species from several geographic regions. All of these species are similar in the presence of the hypomerai glandular fovea (i in Fig. 26C and 27A, B) and the associated exocrine gland cluster (Fig. 26C:j), and similar in most other ventral and leg features (described below).

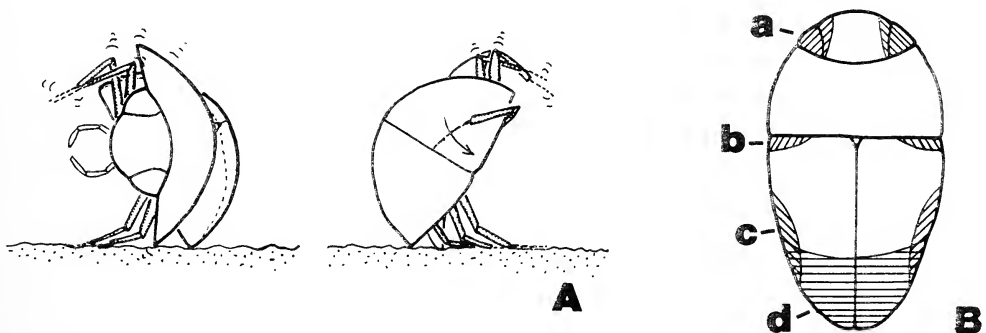


Fig. 25.—*Limnebius piceus*, schematic. A. Beetle balanced on edge, the tibiae of the left legs resting on the surface of a wet leaf, the right legs performing secretion-grooming, anterior (left) and posterior aspects. B. Dorsal areas groomed by legs: (a) protibia and protarsus, (b) protibia, (c) mesotibia, (d) metatibia and metatarsus.

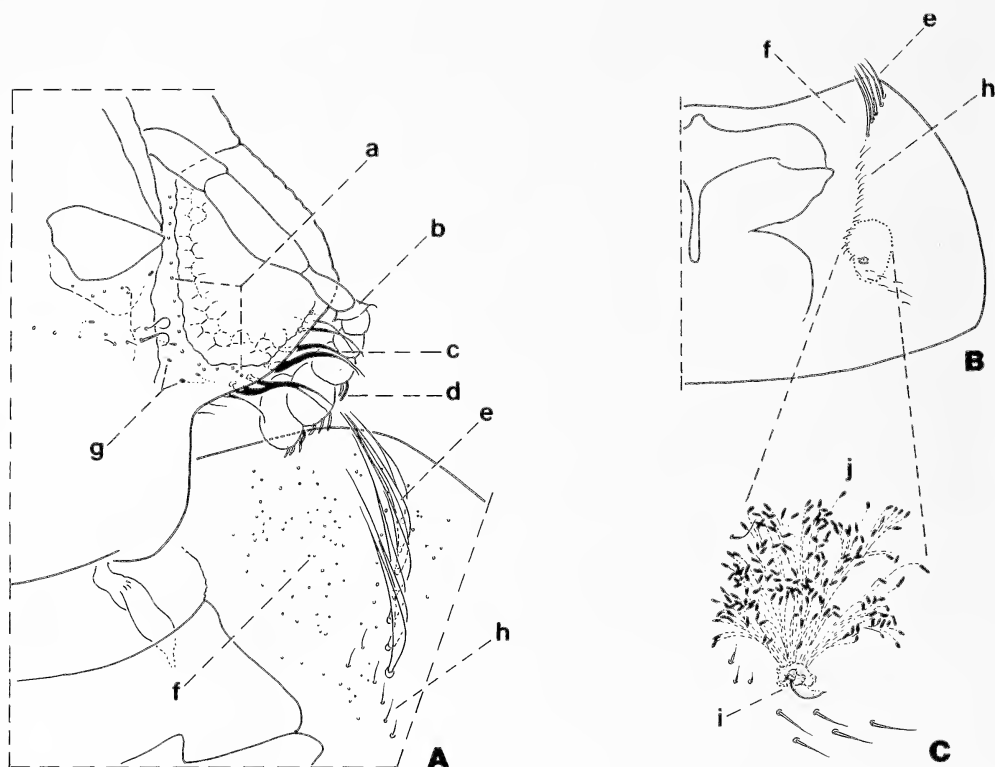


Fig. 26.—*Limnebius truncatellus*. A. Head and adjacent area of prothorax, ventral aspect of left side showing external cuticular features and internal end-apparatus (g) and ductules of exocrine glands. B. Prothorax, ventral aspect of left side. C. End-apparatus and ductules of hypomeral exocrine gland cluster. Structures: (a) periocular exocrine pores, (b) cupule article of antenna, (c) postocular antennal pocket setae, (d) sensilla of antennal club, (e) hypomeral antennal pocket setae, (f) antennal pocket, (g) end-apparatus of exocrine glands, (h) marginal setae of hydrofuge hypomeron, (i) hypomeral glandular fovea, (j) end-apparatus and ductules of hypomeral exocrine gland cluster.

Given these similarities, it seems reasonable to assume that the behavior of *L. piceus* described below is generally representative for the genus. Males of some species of *Limnebius* have highly modified metatibiae. It remains to be determined if this sexual dimorphism relates in some way to secretion-grooming. The metatibiae of *L. piceus* are similar in the sexes.

Secretion-grooming is performed with the beetle "on edge" (Fig. 25A), the legs on one side having the tibiae resting on a wet surface, and the "free" legs on the other side doing the secretion-grooming. Sometimes the beetle (before going on edge) actively moves the mouthparts. Perhaps this behavior serves to spread secretions produced by glands within the mouthparts; it may also serve to remove water by swallowing.

When the beetle is on edge, the prothorax is extended and turned relative to the pterothorax. This positioning of the prothorax "opens" the area around the mesothoracic spiracles, which are located in the intersegmental membrane separating the notal projection of the prothorax and the mesosternum. This position also makes it possible for the legs to contact the posteroventral margin of the

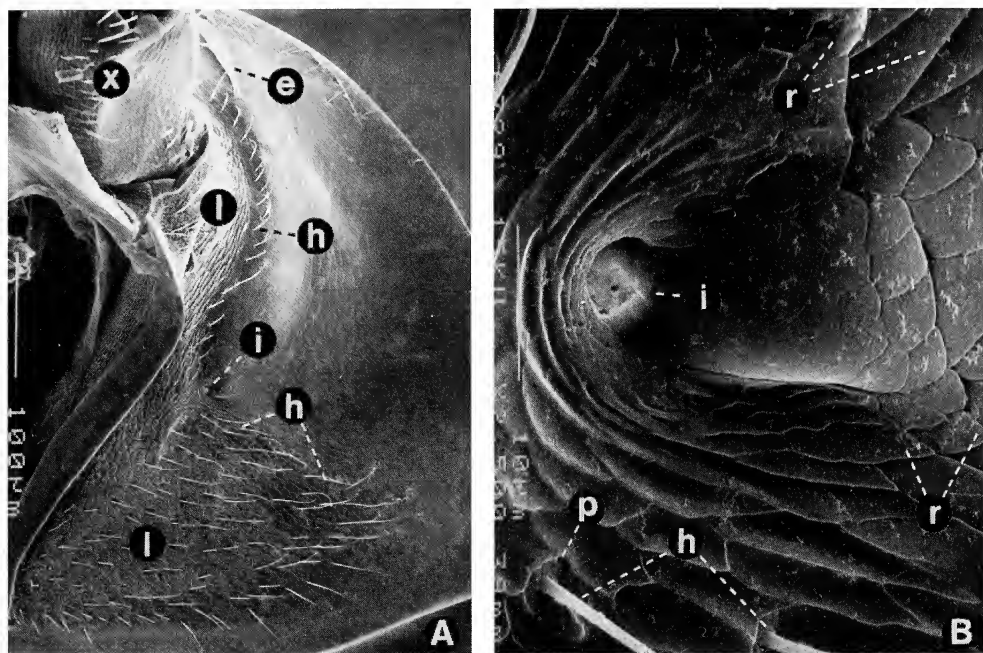


Fig. 27.—*Limnebius truncatellus*. A. Hypomerite, ventral aspect of left side. B. Hypomerite glandular fovea and associated cuticular features. Structures: (e) hypomerite antennal pocket setae, (h) marginal setae of hydrofuge hypomerite, (i) hypomerite glandular fovea, (l) microspiculate hydrofuge, (p) exocrine pore, (r) microreticulation, (x) procoxa.

prothorax and the anterior margin of the elytron, two surfaces which are normally in contact with one another.

The protibia principally rubs four locations: (1) the undersurface of the head, along the antennal groove beneath the eye; (2) the back of the eye, the stroke continuing forward over the top of the eye (Fig. 25B:a); (3) the anterior part of the hypomerite, over the antennal pocket setae (e in Fig. 26A, B and 27A); and (4) over the smooth anterior margin of the elytron (Fig. 25B:b).

Both the profemur and the mesofemur are repeatedly rubbed into the juncture of the prothorax and the mesothorax, and against the area of the hypomerite glandular fovea. Sometimes this rubbing occurs in an alternating pattern, first one leg and then the other. Both the pro- and mesofemur have a distal spine cluster (Fig. 22A, 23A) which contacts the glandular fovea and the surrounding cuticle. The distal spine clusters of both the pro- and mesofemora have some apically flattened and blunt spines, apparently shaped to facilitate spreading the exocrine secretion. In addition to the distal spine cluster, the mesofemur has a unilinear row of spines on the upper surface. These spines are likely involved in rubbing the cuticle during movements in and out of the glandular fovea area.

From time to time the front and middle legs engage in mutual rubbing. This rubbing involves both the femora and tibiae, usually the opposing faces. The anterior face of the mesofemur is provided with short spiniform setae (Fig. 23A) which are involved in the mutual rubbing with the profemur.

The protibial rubbing of the anterior margin of the elytron (mentioned above) occurs as the profemur is rubbed into and out of the exocrine invagination area

of the notal projection. The area of the elytron rubbed (Fig. 25B:b) is the extremely smooth anterior margin that the posterior margin of the prothorax slides over when the beetle is in a "normal" body position.

The mesofemur, after being rubbed into the glandular fovea area, is rubbed backwards along the basal part of the elytral epipleuron. In the same motion, the mesotibia rubs the metasternum, stroking backward and outward. Infrequently, the mesotibia is raised over and stroked backward on the lateral upper surface of the elytron (Fig. 25B:c).

The metatibia rubs along the elytral epipleuron. In addition, the metatibia and the metatarsus stroke backward on the upper surface of the elytron (Fig. 25B:d). The tarsus, which is long enough that the tarsal claws reach to the suture between the elytra, rubs a larger surface area than does the metatibia.

One observation was made of partial grooming while the beetle was in the water. First, while obtaining air at the surface of the water, the bubble is made very large by separating the elytra and the abdomen, thereby forming a large bubble under the elytra. After going beneath the water's surface, the elytra and the abdomen are brought back together, forcing the bubble into the prothoracic and head area. In this enlarged bubble the front leg performs grooming movements.

ESDS Cuticular Components.—Like *Hydraena*, the exocrine gland concentration in *Limnebius* is located in the prothorax. However, the organization of the glands with respect to the external cuticular features, and the form of these structures, bear no resemblance to those of *Hydraena*. Although the postocular area has setae that form part of the antennal pocket, these setae appear not to be homologous with the psd-setae of *Ochthebius*.

Hypomeral Glandular Fovea.—The hypomeral glandular fovea is located on the hypomeron, at the margin of the microspiculate hydrofuge (i in Fig. 26B, C and 27). This fovea is supplied by many ductules of the hypomeral exocrine gland cluster (Fig. 26C:j). Cuticular microreticulations (Fig. 27B:r) "fan out" from the glandular fovea such that secretions issuing from the fovea could be spread in both directions, along the lateral margin of the hydrofuge area.

Hypomeral Hydrofuge.—The anterior part of the hydrofuge hypomeron is bordered by a row of marginal setae (Fig. 26:h, 27:h). Similar setae are sparsely distributed over the posterior part of the hydrofuge hypomeron. An exocrine pore is located at the base of some of these setae (Fig. 27B:p).

Antennal Pocket.—The shallow antennal pocket is bordered by a row of about seven closely spaced antennal pocket setae (Fig. 26A:e, 27A:e). No concentration of exocrine gland end-apparatus was found associated with these setae.

Postocular Structures.—The posteroventral margin of the eye is bordered with postocular antennal pocket setae (Fig. 26A:c). Neither a concentration of end-apparatus, nor a secretion sulcus or other kind of secretion reservoir, was found associated with the postocular antennal pocket setae. Only a few singular end-apparatus (Fig. 26A:g) were found. Periocular exocrine pores (Fig. 26A:a) are present.

Femoral Setae.—The stout femoral setae of *L. piceus* (Fig. 22A, 23A, 24A) are in positions consistent with the secretion-grooming behavior. Some setae of the profemoral distal spine cluster are specialized, being flattened and apically blunt, most likely to increase efficiency in spreading secretions of the hypomeral glands.

The details of the distal spine clusters of *Limnebius* differ from those of *Ochth-*

ebius, and the spine clusters rub different body regions in the two genera. This evidence supports the position that the distal spine clusters of *Limnebius* and *Ochthebius* are independently derived.

SYSTEMATICS OF THE FAMILY HYDRAENIDAE

In my monograph of the western hemisphere members of the family (Perkins, 1981), I proposed a very preliminary phylogenetic classification. At that time I suspected that several new genera awaited description, "most likely South African and Australian" (p. 481), and decided to limit the number of genera I treated to 11. The number of genera now known is 37 and, as one would suspect, changes in the proposed phylogeny and classification are required.

More importantly, we now have a much more complete understanding of a critical aspect of the functional morphology of the family; that is, the hypomeral and postocular components of the antennal pocket and the ESDS in its various manifestations.

Hansen (1991) recently reviewed the genera known at that time, proposed groupings of those genera, and discussed several aspects of my proposed (1981) phylogeny and classification. Hansen's (1991) classification and my present classification are comparatively summarized in Figure 71. Hansen's (1991) paper is an excellent catalogue that resolves several nomenclatorial tangles and provides a useful habitus illustration of a representative of almost all genera then known. However, Hansen's (1991) generic (re)descriptions do not present new characters to reveal the relationships of the genera—perhaps a measure of the difficulties posed by this family. The result was, after declaring some of my 1981 groupings as symplesiomorphous, to "force" other genera into those groups.

Some of the characters I used in 1981 have now been superseded by stronger characters, but the higher-level relationships that I tried to emphasize in 1981 remain unchanged: the Ochthebiinae is a separate subfamily, *Limnebius* is more closely related to *Hydraena* than to *Ochthebius*, and the relatively primitive forms I placed in the Hydraenidini are still grouped together, with the exception of *Coelometopon* (moved to a new tribe).

The classification proposed herein is influenced greatly by the new characters of the antennal pocket morphology and the comparative study of the ESDS. The extent to which these new characters have informed the classification will be very apparent from a comparison of the taxonomic key of Hansen (1991) with the keys presented herein.

Although many of the relationships of the genera have been clarified, the relationships among groups at the tribal and subtribal level are still problematic and require the discovery of new character systems. The tribes and subtribes adopted herein emphasize the individuality of the groups, and also reflect the rather high probability that additional new genera, members of the present tribes and subtribes, will be discovered.

Subfamily Ochthebiinae Thomson Tribe Ochtheosini, **new tribe**

This new tribe is erected for *Ochtheosus*, a new genus known from one fungus-dwelling species from Chile. This genus retains several primitive characters: (1) it is the only known member of the subfamily with 11 antennomeres, the ancestral number for the family; (2) the lacinia and galea, in contrast to all other Ochthe-

biinae, retain the presumed ancestral condition for the family: brush-like, bearing many slender setae; and (3) the aedeagus has the ancestral condition of fully developed parameres.

In addition to these primitive features, *Ochtheosus* is the only Ochthebiinae to retain the primitive condition for the tentorium. Previously I (Perkins, 1981) suggested that the presence of a "gular sclerite" in the Ochthebiinae was a primitive condition in the family, based on its presence in the outgroups Staphylinidae and Hydrophilidae. However, after studying transparency mounts of representatives of those two families, I conclude that the gular "sclerite" is a secondarily derived feature. In many groups its formation is associated with the posterior elongation of the head to form a "neck." In the Ochthebiini this "sclerite" has resulted from changes associated with the internal strengthening of the anterior part of the tentorium. Therefore, the gular "sclerite" of the Ochthebiini is not homologous with the gular "sclerite" of any other groups, including the Staphylinidae and Hydrophilidae.

The reinforcing of the tentorium, resulting in the formation of an anterior wall with a central "foramen" through which nerves pass (see Perkins, 1981:fig. 151), is absent in *Ochtheosus*. Therefore, the wall structure is a very strong synapomorphic character of the tribe Ochthebiini. This strengthened tentorium is probably structurally related to the other strong synapomorphic character of the Ochthebiini: the lacinia bears enlarged, stout apical teeth.

According to Stickney's (1923) interpretation of the tentorium of Coleoptera, in the ancestral condition the tentorium had, on each side, a small mesial extension termed the laminotentorium. According to this interpretation, ancestrally the laminotentoria were separated one from the other; secondarily, in many unrelated groups, the laminotentoria become fused on the meson.

The hypothetical ancestral (unfused) condition is present in the Orchymontinae and in the Ochtheosini, reflecting the basal origin of these groups. In nearly all Prosthetopinae and (apparently all) Hydraeninae the laminotentoria are fused on the meson, and produced ventrad (in varying degrees; especially developed in some Hydraeninae) as two projections. According to Stickney (1923:39), the condition of fused laminotentoria with ventrad projections is present in many (unrelated) families of beetles. In other words, by this interpretation, the fused condition has independently evolved many times. Rarely in the Prosthetopinae, such as *Prosthetops nitens*, the laminotentoria are not fused; this may be a secondary condition related to the broad head shape.

Ochtheosus, new genus

Type Species.—*Ochtheosus fungicolus*, new species.

Diagnosis.—Recognized among Ochthebiinae by the 11 articles of the antenna, the prominent ocelli located near the midline, the convex and setose dorsum, the ventrally directed maxillary palpi, the shape of the mentum, the small dentiform mesosternal intercoxal process, the large metasternal tabella with median concave impression, the lack of a lateral hyaline border, and features of the antennal pocket.

Description.—**Antennal Pocket**. The subocular antennal groove is smooth, relatively wide, and has very few, ca. six, exocrine pores. The postocular area has a low transgenal ridge demarking the posterior limit of the antennal groove. A very small concavity is present where the transgenal ridge joins the eye margin. No exocrine pores were found associated with the ridge or concavity. The

postocular pubescence is well developed and of the reticulate type, whereas the genal pubescence is sparser. Periocular pores were not found on the one specimen studied.

The hypomerical part of the antennal pocket is moderately well developed, its posterior limit well defined by a transverse ridge. The pocket is microreticulate, except the lateral margin, has numerous exocrine pores, and is nonpubescent except the medial margin. The lateral margin of the pocket forms a strong ridge, but its free edge does not extend to form a hypomerical hyaline border; anteriorly and posteriorly this ridge is contiguous with the corresponding hyaline borders.

The wet-hypomeron is smaller than the bubble-hypomeron, and bears a few strong setae similar to those on the dorsum. A small cluster of short, acute asperites (presumed antennal cleaner) is located on each side of the prosternum, at the margin of the antennal pocket. The profemur has small spines over most of the upper surface; these spines are not organized to form a distal spine cluster such as is present in *Ochthebius*.

Other Characters. Form convex, head deflexed. Dorsum, especially relief of pronotum, strongly setose, each seta with round granule at base. Ocelli prominent, located near midline. Antennomeres 11 (six + club). Maxillary palpi short, arching, with apex directed ventrad; second article slender, slightly arcuate; third article suboval, much wider than other articles; fourth (last) article very slender, slightly shorter than third. Mentum as wide as long. Pronotum with discal relief almost Y-shaped (apical part U-shaped); anterior and posterior hyaline borders narrow, lateral absent. Elytra with even-numbered interseries at least in part with setose granules, sometimes granules joined and elevated to form costae or callosities. Prosternum narrow in front of procoxae, with low midlongitudinal carina. Hypomeron, on ventral face, with well-developed carina forming margin of antennal pocket. Mesosternum with small dentiform process between mesocoxae. Metasternum with large transverse tabella with large median concavity. Intercostal sternite small, triangular. Legs short, tarsi very short, five-five-five. Hydrofuge pubescence present on postocular area, bubble-hypomeron behind antennal pockets, medial margin of antennal pocket, notal postcoxal projections, mesosternum, metasternum (except tabella), and first and anterior part of second abdominal sterna.

Etymology.—Greek *ochthe* (mountain) plus *eos* (dawn); gender masculine.

Ochtheosus fungicolus, new species

(Fig. 58A)

Type Material.—Holotype male and one paratype of each gender with same data: Chile: Osorno Province, Puyehue Nat. Pk., Anticura, Repucura trail, 500m, bracket and soft fungi, berlese, 19.xii.1984, S. and J. Peck, P#85-41, FMHD#85-926; deposited in FMNH.

Description.—Size (mm × 100; length/width): body 155/80, head 36/54, pronotum 42/69, elytra 110/80. Color dark brown, dorsal setae and ocelli testaceous. Labrum deflexed, wider than long, apical margin with dense fringe of golden setae; apicomediaally shining and with small dentiform process in males, shining and simple in females. Frons and clypeus densely granulose and setose. Pronotum more densely setose on reliefs, granulate throughout except shining basal band; lateral margin granulose and setose, sides converging posteriorly. Elytra punctuation irregular, especially in distal half and laterally, with "extra" series between costae, noncostate intervals shining. Granulate costae on derivatives of even-numbered intervals as follow: second: present in front of and behind discal saddle; fourth: sinuate, interrupted over short distance near apical third; sixth: complete, sinuate, apically joining costa of fourth; eighth: present over basal half, straight. Elytral margin granulate. Hypomeron with antennal pockets shining, slightly wider than widest part of wet-hypomeron. Metasternal tabella tapering and shining laterally, sparsely pubescent, median fovea slightly wider than mentum, micro-punctulate, anterior margin of fovea formed by a thin wall that connects with short apicomedian ridge. Wing reduced to small lobe. Aedeagus (Fig. 58A) with well-developed parameres and short distal process; length 0.36 mm.

Etymology.—Named in reference to the microhabitat.

Discussion.—One additional female specimen of *Ochtheosus* was studied; this specimen differs slightly from the paratype female and may represent a second species: Aisen Province, 33 km E Pto. Aisen, Rio Simpson N. P., 70m, 26.i.1985, forest sifted bracket fungi, S. and J. Peck, P#85-104, FMHD#85-987.

Subtribe Ochthebiina Thomson

This subtribe is erected for the genera *Ochthebius* (type genus), *Gymnochthebius*, *Hughleechia*, *Gymnanthelius*, *Aulacochthebius*, and *Micragasma*. These genera, except perhaps *Micragasma* (see below), have a derived antennal pocket consisting of a postocular area with a secretion distribution sulcus and elongate postocular secretion distribution setae; and a prothorax with a "full complement" of hyaline borders, and comparatively elongate hap-setae.

Hughleechia, judging from its unusual postocular secretion sulcus, probably diverged early in this clade. *Micragasma* Sahlberg is a very rare, monotypic genus from Greece, for which I have had only a few specimens to study. This genus has the full complement of hyaline borders, and a pronotal shape like *Ochthebius* (*Asiobates*). However, based on the few specimens available for study, the postocular area appears to lack both a discrete secretion sulcus and postocular secretion distribution setae. Additional study, with SEM, may reveal that *Micragasma* is another basal group, diverging early in the evolution of the Ochthebiina.

Genus Ochthebius Leach

A determination of the phylogenetic classification of the genus *Ochthebius* has eluded taxonomists from the earliest workers to the most recent. Early workers "split" the genus into many subgenera, later workers "lumped" some and "split" others (see discussion in Perkins, 1981). Recently, several subgenera were synonymized by Hansen (1991) in a review catalogue.

The morphology and behavior elucidated herein provide integrated character systems that clarify the phylogenetic relationships in this group (at least partially; see discussion of *Gymnochthebius*). It is proposed that the genus *Ochthebius* be restricted to species having all the cuticular components of the ESDS, including the (1) postocular secretion delivery (psd-) sulcus, (2) postocular secretion delivery (psd-) setae, (3) hypomeral antennal pocket (hap-) setae, (4) hypomeral hyaline (hh-) border, and (5) lateral hyaline (lh-) border. These species will also have the exocrine glands that empty into the psd-sulcus, the leg-grooming setae, and grooming behavior patterns utilizing these leg setae.

Examples of variations in the ESDS components of *Ochthebius* (as herein defined) are discussed below. Of the species studied, the range of variation in the number of psd-setae is two to eight, with most species having four. The range of variation in the number of hap-setae is three to seven, with most species having either four or five.

Subgenera of *Ochthebius* herein considered valid are thought to be basally derived within *Ochthebius*. Current subgenera are placed into synonymy when found to have ESDS components that are connected by morphocline intermediates to the nominate (and less derived) subgenus (e.g., see *Calobius*, *Cobalius*, and *Notochthebius* below).

Species with ESDS components that differ from those described above, and appear not to represent systems clearly derived from that of *Ochthebius*, are recognized as distinct genera (e.g., see *Enicocerus* and *Aulacochthebius* below).

Finally, species lacking some (or all) ESDS components (and this absence not appearing to be a result of secondary loss), are recognized at the generic level, separate from *Ochthebius* (e.g., see *Protochthebius* and *Neochthebius* below). Possession of a plesiomorphic condition cannot be used to infer the common ancestry

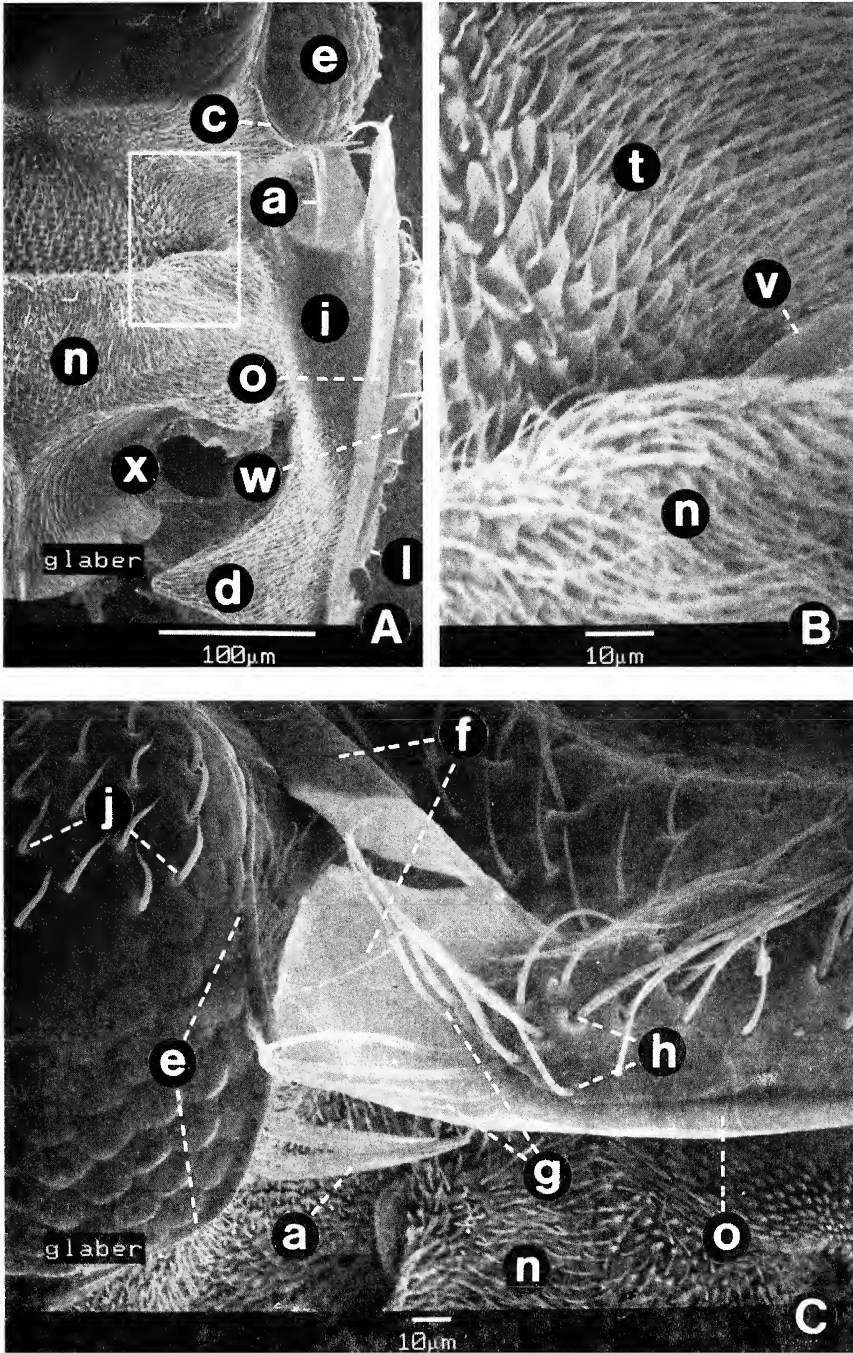


Fig. 28.—*Ochthebius glaber*. A. Venter of left side of head and prothorax. B. Rectangular area of A, enlargement. C. Lateral view of eye and prothorax contact area. Structures: (a) psd-setae, (d) notal postcoxal projection, (e) eye, (f) ah-border, (g) hap-setae, (h) anterolateral pronotal setae, (i) hypomerall antennal pocket, (l) lh-border, (n) prosternum, (o) hh-border, (j) setae of dorsal surface of eye, (t) genal asperite hydrofuge, (v) cervical sclerite, (w) wet-hypomeron, (x) procoxal cavity.

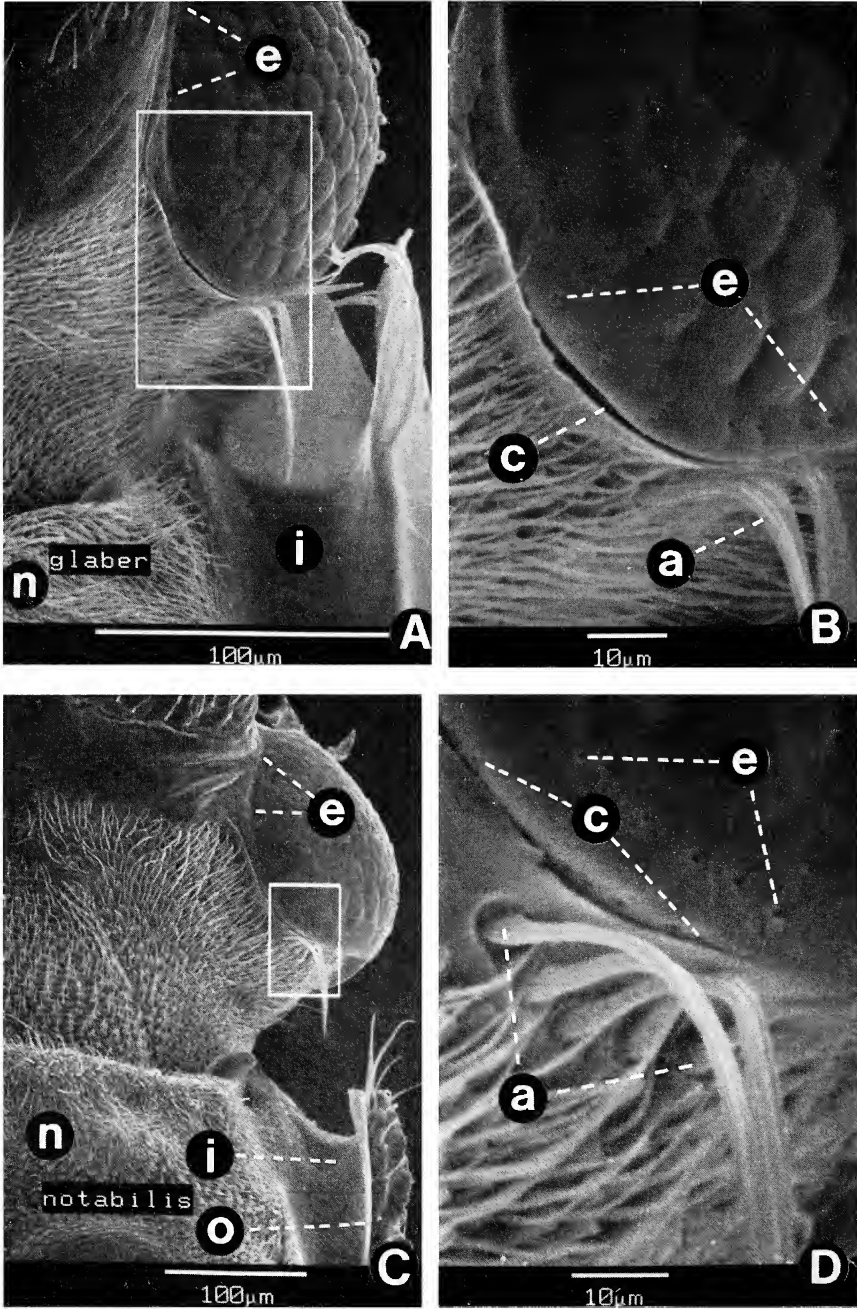


Fig. 29.—*Ochthebius*. A. *O. glaber*, venter of left side of head and prothorax. B. Rectangular area of A, enlarged. C. *O. notabilis*, venter of left side of head and prothorax. D. Rectangular area of C, enlarged. Structures: (a) psd-setae, (c) psd-sulcus, (e) periocular exocrine pores, (i) hypomeran antennal pocket, (n) prothorax, (o) hh-border.

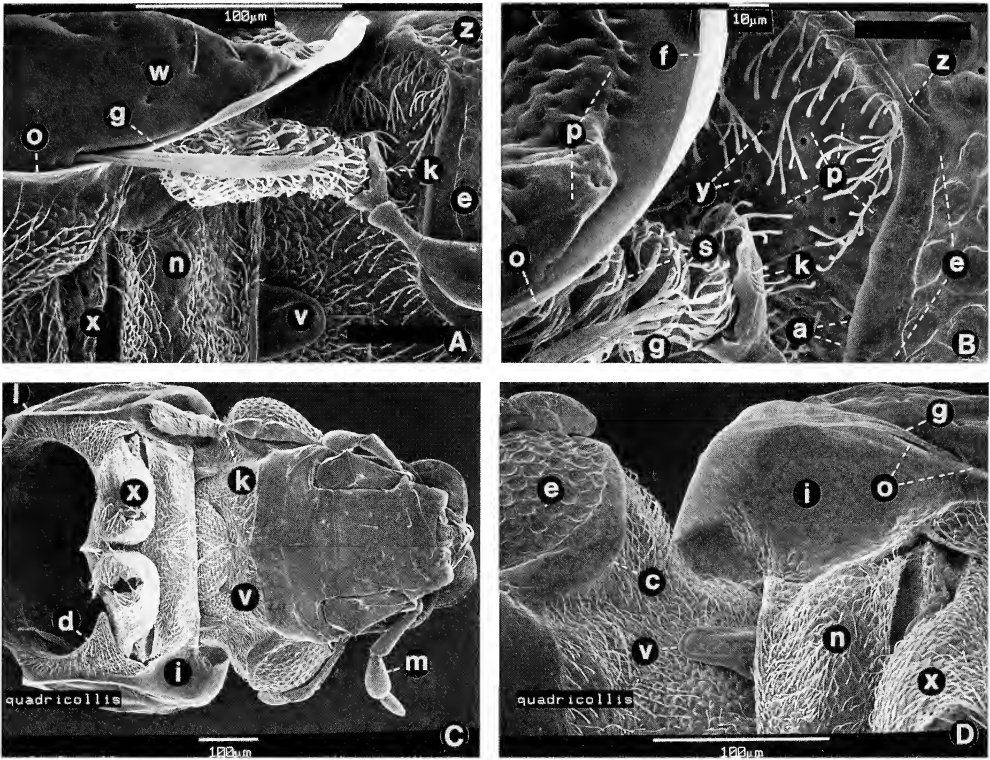


Fig. 30.—*Ochthebius quadricollis*, treated with sodium hydroxide. A, B. Postocular area and adjacent prothoracic structures, right side. C. Venter of head and prothorax. D. Postocular area and adjacent prothoracic structures, left side. Structures: (a) sockets of psd-setae, (c) psd-sulcus, (d) notal postcoxal projection, (e) periocular exocrine pores, (f) ah-border, (g) hap-setae, (i) hypomer al antennal pocket, (k) cupule article of antenna, (l) lh-border, (m) maxillary palpus, (n) prosternum, (o) hh-border, (p) exocrine pores, (s) sensilla of antennal club, (v) cervical sclerite, (w) wet-hypomeron, (x) procoxa, (y) sockets of missing setae, (z) sulcus of (?)periocular pores.

of species with that condition. Therefore, detailed study should be given forms that lack ESDS components.

Subgenera *Calobius* Wollaston and *Cobalius* Rey, **new synonymy**

The effectiveness of the ESDS in revealing phylogenetic relationships, and mistaken methods, is well demonstrated by the so-called subgenera *Calobius* and *Cobalius*. The ESDS components of *Calobius*, represented by *Ochthebius quadricollis*, differ from *Ochthebius* (sensu stricto) in three major respects (the type species, *Calobius heeri* Wollaston, is a junior synonym of *O. quadricollis*). All of these features, relative to the ESDS of *Ochthebius* (sensu stricto), must be considered *derived* conditions.

The ESDS components of *O. quadricollis* (Fig. 2B; 30; 33A, B) are as follow: (1) the psd-sulcus (Fig. 33B:c) is smaller, the postocular pores at the sulcus being concentrated in a smaller area; in whole mounts, this area appears distinctively more heavily sclerotized and more complex than the same area in *Ochthebius* (sensu stricto); (2) the hap-setae (Fig. 2B:g) arise more posteriorly, opposite the trochanter; however, these hap-setae are very long and their tips attain a position—

contacting the psd-setae—similar to that attained by their homologues in *Ochthebius* (sensu stricto); and (3) the hh-border is not as wide as is generally found in *Ochthebius* (sensu stricto) (Fig. 30:o).

The two “subgenera,” *Calobius* and *Cobalius*, were recently revised by Jäch (1989, 1993), who considered them distinct and unrelated. Jäch (1993:33) states, “*Calobius* is obviously not very closely related to any other genus or subgenus of the subfamily Ochthebiinae,” and “. . . a generic status for *Calobius* could be taken into consideration.” Regarding *Cobalius*, Jäch (1989:41) remarked that “It differs from all other subgenera of *Ochthebius* by the peculiar dentation of the elytral margin.”

In his revision of *Cobalius*, Jäch (1989) described a new species, *Ochthebius* (*Cobalius*) *celatus*. Thorough study of this species, however, reveals that the ESDS is virtually identical to that of *O. (Calobius) quadricollis*. This evidence, which is supported by the overall external resemblance of these two species (except the denticulate margin of *O. celatus*, see below), clearly indicates that these two species are very closely related.

Jäch (1992a:7) used “a very large head” to characterize *Calobius*, and in 1993 (p. 33) stated that “*Calobius* is easily distinguished from other subgenera of *Ochthebius* by the wide head and pronotum, by the strongly reduced epipleura, which are ended before the middle of the elytra and by the missing explanate margin of the elytra. . . .”

However, measurements of *O. quadricollis* show that the length/width proportions of the head and pronotum each differ insignificantly, or not at all, from the proportions found in other *Ochthebius* (sensu stricto). This is also true of the proportions of the elytra. In other words, neither the head nor the pronotum is wide. Rather, it is the pterothorax (and elytra) that are derived, via size reduction, consistent with the reduced condition of the elytral epipleura and loss of the explanate elytral margin.

Ochthebius serratus Rosenhauer and *Ochthebius adriaticus* Reitter, two other species that Jäch (1989) placed in *Cobalius* (based on the superficial character of denticulate elytral margins), are, in fact, with respect to the placement of the hypomer al antennal pocket setae, morphocline intermediates between *Ochthebius* (sensu stricto) and “*Calobius*” *quadricollis*.

The morphocline of hap-setae number and placement in this clade is as follows. In the ancestral condition, the hap-setae are closely clustered at the anterior angle of the hypomeron (opposite the anterior margin of the prosternum) and usually four or five in number (e.g., *O. marinus*; Fig. 31A). In *O. serratus* the hap-setae are five in number, and in a line, with the socket of the most posterior seta of the row being opposite, or nearly so, the midlength of the prosternum (Fig. 31B). In *O. adriaticus* and *O. subinteger* the hap-setae are reduced to four, and are located more posteriorly, opposite the trochanter of the front leg (Fig. 31C, D). Finally, in *O. quadricollis*, *O. celatus*, and *O. lejolisi* (the type species of *Cobalius*) the hap-setae are reduced to three in number, and these are positioned opposite the trochanter (Fig. 2B; 30A; 31E, F).

The polarity of this morphocline is not based primarily on an outgroup comparison. It simply makes more sense for the hap-setae to have initially evolved where they would be of use, despite their comparatively small size. This location is at the anterior extreme of the hypomeron, where the tips of the setae (even when quite small) could “bridge the gap” at the marginal area of the bubble, between the antennal pocket and the postocular area of the head. This ESDS

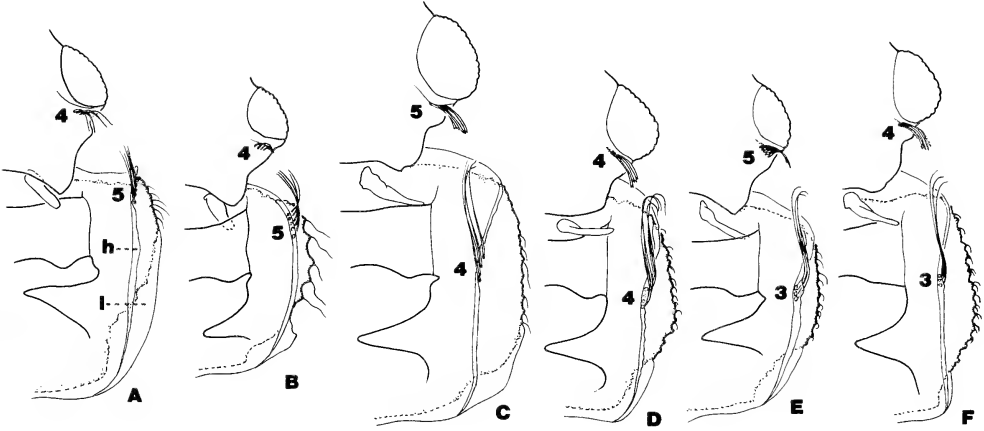


Fig. 31.—*Ochthebius* spp., ventral aspect of head and prothorax, left side, illustrating ancestral condition (A) and morphocline of hap-setae of *quadricollis* group species. Numbers of psd-setae and hap-setae indicated. A. *O. marinus*, hh-border (h) and lh-border (l). B. *O. serratus*. C. *O. adriaticus*. D. *O. subinteger*. E. *O. celatus*. F. *O. lejolisi*.

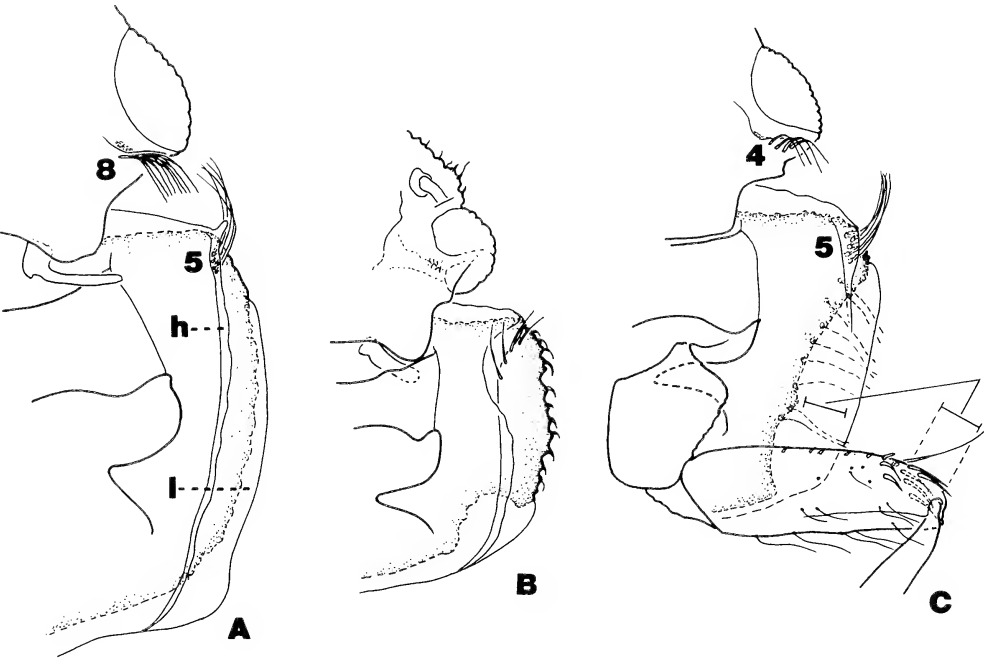


Fig. 32.—Ventral aspect of head and prothorax, left side. Numbers of psd-setae and hap-setae indicated. A. *Ochthebius capensis*, hh-border (h) and lh-border (l). B. *Micragasma paradoxum*. C. *Ochthebius spatulus*, illustrating the loss of posterior part of the hh-border, and the correlation of width of the lh-border and length of setae in the profemoral distal spine cluster.

component morphocline clearly reveals that *Calobius* is a comparatively recent derivative within the species group *Calobius* + *Cobalius*.

The elytral and pronotal denticles present in *O. celatus* Jäch and, for example, "*Cobalius*" *serratus* Rosenhauer, could, of course, be interpreted as being independently derived. However, given the morphocline relationship of the ESDS of *serratus*–*celatus*–*quadrifollis*, a more likely morphological history is that the denticulate margins were inherited from the common ancestor of *Calobius* + *Cobalius*. Of course it is difficult to have appropriately shaped margins when margins do not exist.

The dorsum of *O. serratus* has the presumed ancestral condition of comparatively rough sculpture, the pronotum being foveate, and the marginal denticles comparatively prominent. In *O. celatus* the dorsum is much smoother, the pronotum virtually nonfoveate, and the denticles smaller. In *O. quadrifollis* the denticles (together with the explanate margin) are lost without a trace.

Correct species-group placement of all of the other species included in Jäch's 1989 revision of "*Cobalius*" requires an examination of the ESDS components of each species. *Ochthebius subinteger* Mulsant and Rey is a member of this group. In the one specimen of this species I was able to study, the left side had four hap-setae, and the right side had three hap-setae (positioned as in *O. quadrifollis* and *lejolisi*). At least two species of this group, *O. adriaticus* and *O. subinteger*, have a derived condition of the psd-setae: the setae are flattened and the apices are blunt and jagged (Fig. 31C, D).

I hereby synonymize both *Calobius* Wollaston and *Cobalius* Rey with *Ochthebius* Leach. The literature citations and type species are given by Hansen (1991) and need not be repeated here.

All members of this clade, which is properly referred to as the *quadrifollis* species group, are apparently halophilic. Some members of the group, for example *O. quadrifollis*, have secondarily developed a more brush-like condition of the lacinia and galea—perhaps reflecting a difference between the microfaunal food sources present in marine rockpools and those present in freshwater microhabitats.

Subgenus *Liochthebius* J. Sahlberg, **new synonymy**

This monotypic subgenus was established for *Ochthebius eburneus* J. Sahlberg, a species from Tunis. Although this species is unusually smooth dorsally, and has an unusually spinose labrum, the pronotal shape is typical of *Ochthebius* (sensu stricto), and the ESDS is clearly a slightly derived variety of the *Ochthebius* (sensu stricto) configuration.

The antennal pocket is relatively wide and smooth, and the wet-hypomerite is, correspondingly, quite narrow. The hypomerite hyaline border, at its posterior extreme, merges with the anterior extreme of the quite narrow lateral hyaline border. There are three psd-setae, apically pointed and of usual length. There are three hap-setae, originating from the anterior extreme of the wet-hypomerite; these setae are slightly longer than usual for the genus (only one specimen, from the type series, was studied). The ESDS components and the dorsal habitus leave no doubt that *O. eburneus* is simply yet another slightly specialized form within *Ochthebius* (sensu stricto). I hereby synonymize *Liochthebius* J. Sahlberg with *Ochthebius* Leach. Refer to Hansen (1991) for literature citations and type species.

Subgenus *Notochthebius* Orchymont, **new synonymy**

The subgenus *Notochthebius* was described by Orchymont for the single South African species *Ochthebius capicola* (Péringuey). The ESDS of *O. capicola* has all of the derived features present in *Ochthebius* (sensu stricto). All hyaline borders are present, and the hap-setae are five in number and clustered near the anterior angle of the hypomeron.

The ESDS of *O. capicola* differs from *Ochthebius* (sensu stricto) in having the derived condition of eight psd-setae (Fig. 32A), and in having the psd-sulcus shorter (like *O. rubripes*; Fig. 34D), with the exocrine pores more concentrated and the internal part of the reservoir more heavily sclerotized (i.e., internally more complex than in *Ochthebius* [sensu stricto]). *Ochthebius capicola* has no characters from which can be inferred a basal origin within *Ochthebius*. *Notochthebius* Orchymont is hereby placed in synonymy with *Ochthebius* Leach. Refer to Hansen (1991) for literature citations and type species.

Subgenus *Nyxochthebius* Orchymont, **new synonymy**

The subgenus *Nyxochthebius* was described by Orchymont for the single Namibian species *Ochthebius rubripes* Boheman. Recently, Perkins and Balfour-Browne (1994) compared some aspects of the dorsal and abdominal morphology of *O. rubripes* and *O. capicola*, and considered *Nyxochthebius* a junior synonym of *Notochthebius*.

The ESDS of *O. rubripes* entirely confirms this relationship and synonymy: the ESDS parts are virtually identical to those of *O. capicola*, including the derived condition of the psd-sulcus (internally complex) and psd-setae (eight in number; Fig. 9; 33C, D). *Nyxochthebius* Orchymont, 1933, is hereby "formally" synonymized with *Ochthebius* Leach, 1815. Refer to Hansen (1991) for literature citations and type species.

Ochthebius (sensu stricto) *capicola* and *O.* (sensu stricto) *rubripes*, the two species comprising the *capicola* group, are found in marine rockpools, as are most (if not all) species in the *quadricollis* group. The evolutionary process of loss of dorsal sculpture has independently occurred in the two groups. As noted above, in the *quadricollis* group the rough ancestral sculpture has been retained by *O. serratus*. In the *capicola* group it is *O. rubripes* that retains the more roughly sculptured dorsum (see also Perkins and Balfour-Browne, 1994).

The internally more complex psd-sulcus of members of the *capicola* group and some members of the *quadricollis* group, together with the unusual habitat of these species, suggests that perhaps species in this microhabitat are experiencing selection for more copious production of the exocrine secretions. This is also suggested by the large number (eight) of psd-setae present in *O. capicola* and *O. rubripes*. The selective elements may be the salinity of the water, the turbulence of the rockpools, or perhaps the kinds of "ESDS fouling" microorganisms present in these rockpools.

Subgenus *Asiobates* Thomson (Fig. 1D, 35)

The ESDS of the subgenus *Asiobates* is very similar to that of *Ochthebius* (sensu stricto). In some species, for example *O. angularidus* (Fig. 1D), the pericocular pores are quite large and well separated from the postocular pores. Addi-

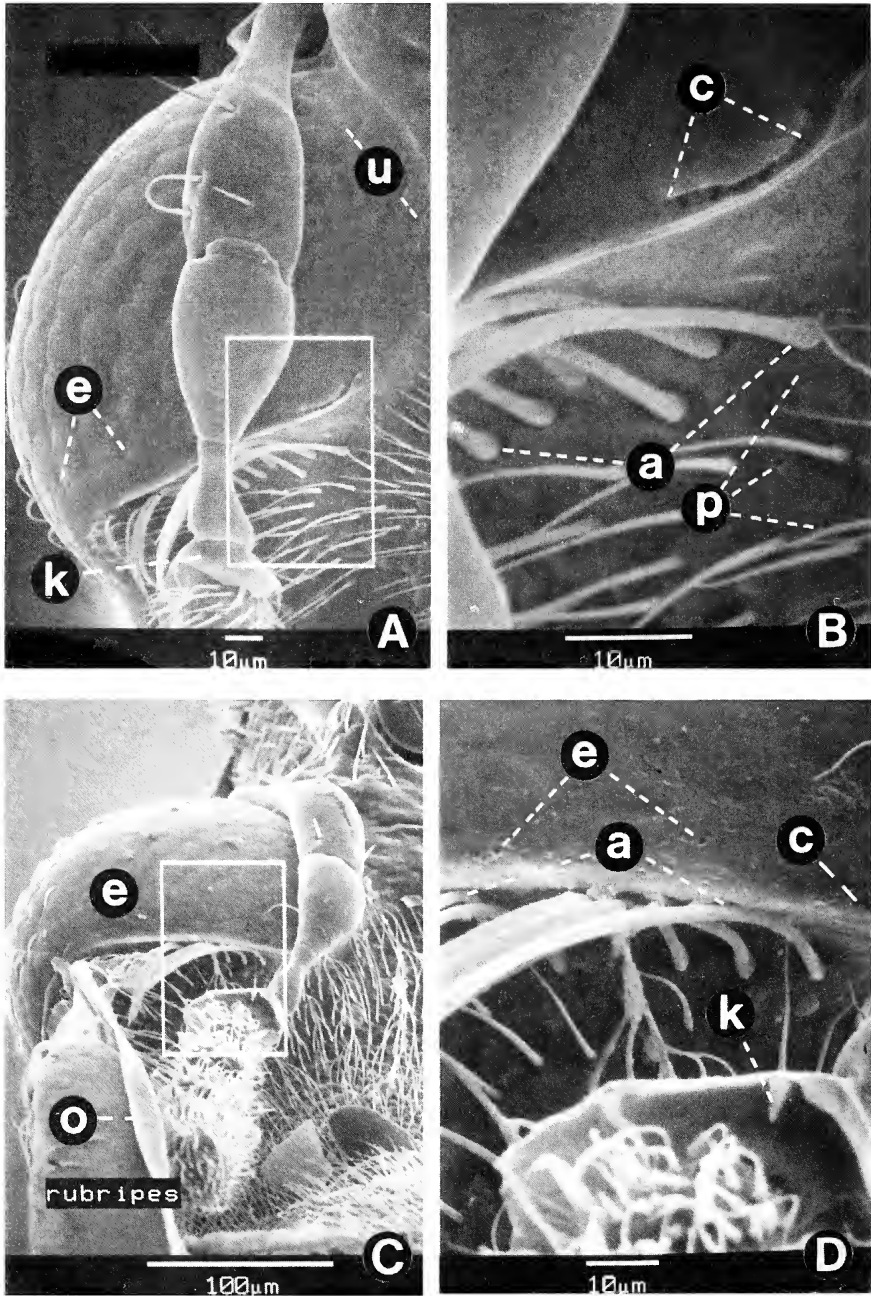


Fig. 33.—*Ochthebius*, venter of eye and adjacent structures. A. *O. quadricollis*. B. Rectangular area of A, enlarged. C. *O. rubripes*. D. Rectangular area of C, enlarged. Structures: (a) psd-setae, (c) psd-sulcus, (e) periocular exocrine pores, (k) cupule article of antenna, (o) hh-border, (p) exocrine pores, (u) subocular antennal groove.

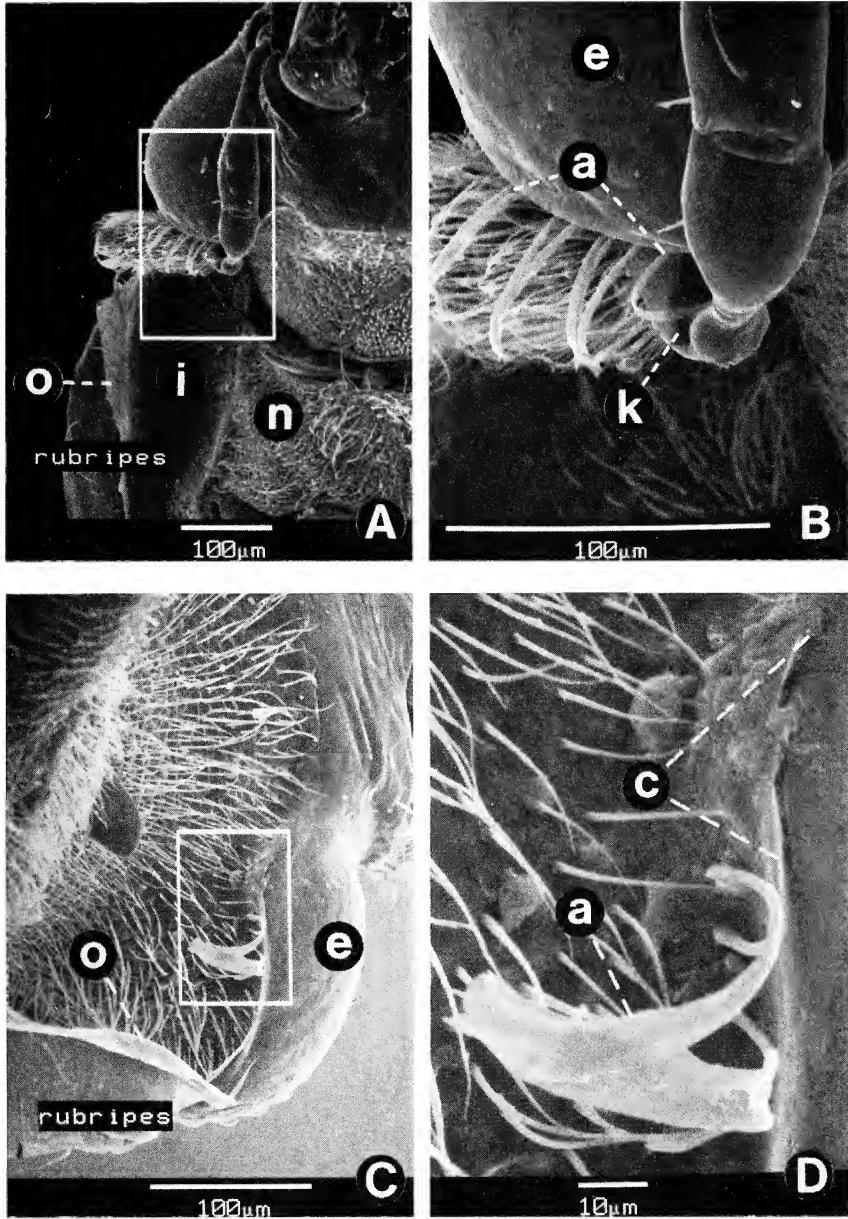


Fig. 34.—*Ochthebius rubripes*. A. Ventral aspect of head and prothorax. B. Rectangular area of A, enlarged. C. Posterior aspect of subocular area. D. Rectangular area of C, enlarged. Structures: (a) psd-setae, (c) psd-sulcus, (d) end-apparatus and ductules of exocrine glands, (e) eye, (i) hypomeral antennal pocket, (k) cupule article of antenna, (n) prosternum, (o) hh-border.

tionally, often the psd-setae are oriented slightly differently than those of *Ochthebius* (sensu stricto), being less sinuate at their bases (Fig. 1D:a, 35B:a).
The psd-setae vary in number from two or three (see *bicolon*, below) to five or perhaps six (in the species studied), with a tendency toward having the posterior

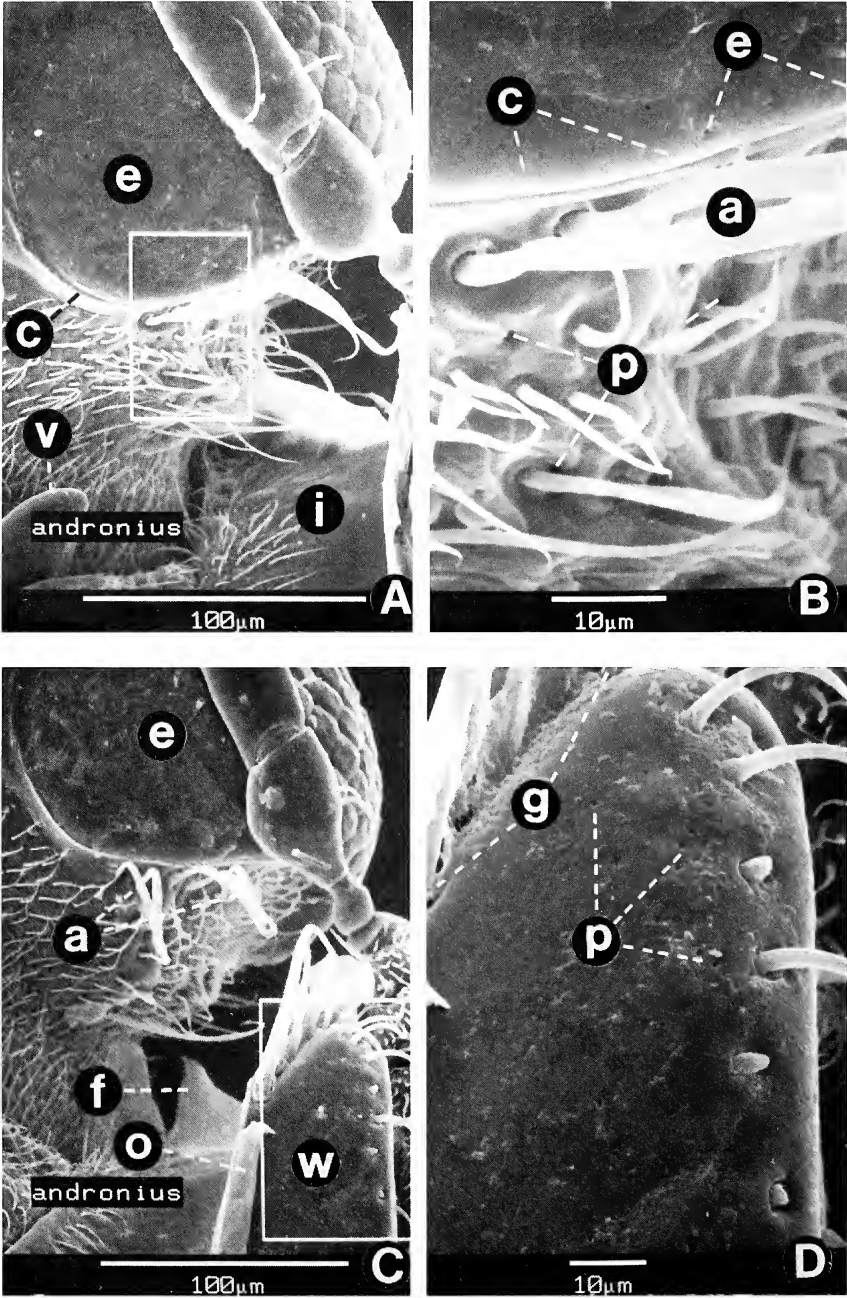


Fig. 35.—*Ochthebius andonius*. A. Venter of eye and adjacent prothorax. B. Rectangular area of B, enlarged. C. Venter of eye and adjacent prothorax. D. Rectangular area of C, enlarged. Structures: (a) psd-setae, (c) psd-sulcus, (d) end-apparatus and ductules of exocrine glands, (e) eye and periocular exocrine pores, (f) ah-border, (g) hap-setae, (i) hypomer al antennal pocket, (o) hh-border, (p) exocrine pore clusters of wet-hypomeron, (v) cervical sclerite.

two or three setae much larger than the anterior setae. The setae are always located at or near the anterior extreme of the hypomerion. The shapes vary, including flattened or nonflattened, the tips pointed, sometimes abruptly so, sometimes elongate and very gradually tapering to form slender tips.

Preliminary comparisons indicate that there is at least some consistency in the number and shape of the psd-setae—at the species-group level—that may be useful for diagnosing members of species clusters that have a more derived condition (e.g., few or many psd-setae, elongate tips, and size differences among the setae).

In *O. bicolon* Germar (the type species of *Asiobates*, *O. rufomarginatus* Erichson, is a junior synonym), there are only two psd-setae (some variation in number might be expected); these setae taper gradually and are not flattened. There are four or five hap-setae, the two most posteriorly placed being much larger than the others. The hh-border is wide at the hap-setae, the latter not extending greatly beyond the hyaline border.

Contrastingly, in *O. angularidus* Perkins there are four psd-setae, less tapering than those of *O. bicolon*. There are five hap-setae, all about equal in length, closely and regularly spaced (in a row), and each extending well beyond the free margin of the hh-border.

Asiobates is retained as a valid subgenus for the following reasons: (1) the monophyly of the group is strongly suggested by the consistent shape of the aedeagus, with the parameres diverging from the main-piece (Perkins, 1981:295); (2) the characteristic pronotal shape, with the posterior sides sharply “excavate”; (3) despite the high morphological diversity and wide geographical range of both *Asiobates* and *Ochthebius* (sensu stricto), there are no known transitional morphocline intermediates (in 1 and 2 above) between them; and (4) there is some evidence suggesting that *Asiobates* diverged basally in *Ochthebius* (see *Micragasma*, below).

The placement of *Homalochthebius* as a synonym of *Asiobates* by Perkins (1981) is corroborated by the ESDS. For example, a species formerly placed in *Homalochthebius*, *O. andronius* Orchymont (Fig. 35) is similar to other *Asiobates* in features of the ESDS, except that there are more psd-setae (five) and more hap-setae (six to eight) than the number present in most species of *Asiobates* (four and four to six, respectively). In other words, the ESDS of members of the “*Homalochthebius*” group represents a derived condition within *Asiobates*.

Genus *Gymnochthebius* Orchymont (Fig. 36, 51C)

Members of *Gymnochthebius* that I have been able to study were found to have a postocular and hypomerion antennal pocket structure very similar to that of *Ochthebius*. For example, in *Gymnochthebius plesiotypus* (Fig. 36) the postocular area has a well-developed secretion sulcus (Fig. 36:c) and secretion delivery setae (Fig. 36:a), and the hypomerion antennal pocket has a hyaline border (Fig. 36:o) and hap-setae (Fig. 36:g) opposite the psd-setae.

However, there are many differences between the two groups, including aedeagal and spermathecal structure (see Perkins, 1981), abdominal vestiture (see *Aulacochthebius*, below), leg structure, and greater development of hypomerion glands in *Gymnochthebius* (described below). The aedeagal and abdominal structures of *Gymnochthebius* suggest a closer relationship to *Aulacochthebius* and

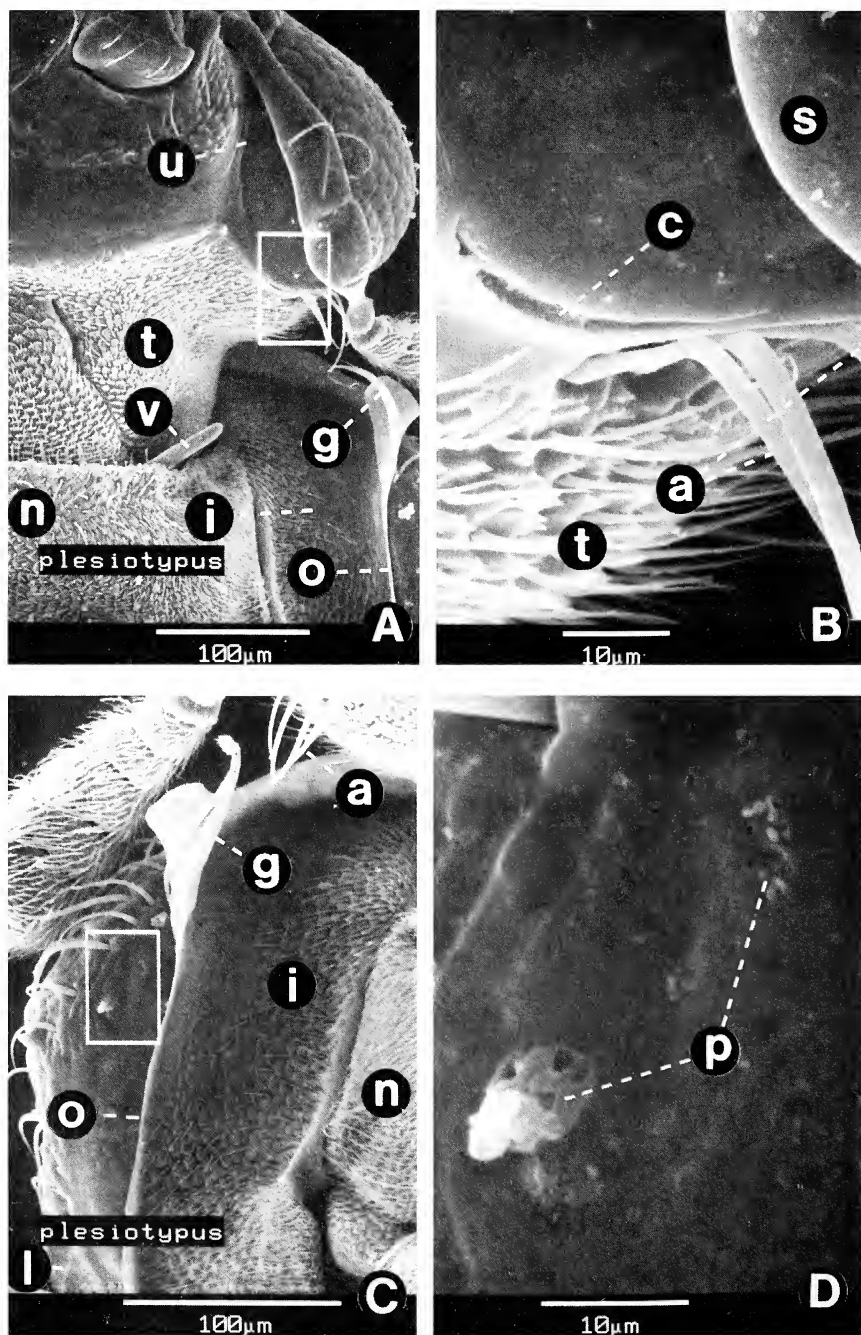


Fig. 36.—*Gymnochthebius plesiotypus*. A. Venter of head and prothorax. B. Rectangular area of A, enlarged. C. Antennal pocket area of prothorax. D. Rectangular area of C, enlarged. Structures: (a) psd-setae, (c) psd-sulcus, (g) hap-setae, (i) hypomer al antennal pocket, (l) lh-border, (n) prosternum, (o) hh-border, (p) exocrine pore clusters, with secretion, (s) second antennomere, (t) genal and post-ocular asperite hydrofuge, (u) subocular antennal groove, (v) cervical sclerite.

Gymnanthelius than to *Ochthebius*. These similarities and differences suggest that *Gymnochthebius* diverged basally within the Ochthebiina. Study of additional species are necessary to discover the full range of variation in the ESDS of *Gymnochthebius*.

The hypomeral exocrine glands of *Gymnochthebius plesiotypus* (Fig. 51C) comprise two types, based on shape of the end-apparatus: (1) spermoid—sperm-shaped (similar to those in Fig. 3), with long ductules relative to the size of the end-apparatus (Fig. 3:b). The pores (Fig. 51C:a) for these glands are solitary, and are present principally in the nonhydrofuge pubescent part of the antennal pocket; and (2) tubuloid—tubule-shaped, with short ductules relative to the length of the end-apparatus. On the wet-hypomeron the pores of these glands are grouped into four distinct clusters, each with about seven pores (Fig. 36C, D; 51C:c, t). Additional tubuloid glands are found singly along the posterior part of the hypomeron.

Genus *Aulacochthebius* Kuwert, **new status**

(Fig. 37)

In *Aulacochthebius* a postocular secretion sulcus (Fig. 37:c) is present. The ridge of the sulcus is continuous with a transgenal ridge (Fig. 37:z); this carina is absent in *Ochthebius*. The psd-setae (Fig. 37:a) are relatively short, slightly widened from base to apex, flattened, and apically fringed. Periocular pores (Fig. 37:e) are present.

The hypomeral antennal pocket (Fig. 37:i) is well developed, smooth, and non-pubescent, except hydrofuge pubescent anteromedially. The hh-border is well developed, contiguous anteriorly with the ah-border, posteriorly passing across the ventral surface of the well-developed lh-border, and contiguous with the ph-border. The hypomeral antennal pocket setae (Fig. 37:g) are well developed, flattened, about five in number, and about twice as long as the hh-border is wide. The wet-hypomeron is well developed. The profemur has a well-defined distal spine cluster, the spines few in number but distinctly larger than other profemoral spines.

This genus is currently being revised by the author. *Aulacochthebius* appears to be most closely related to *Gymnochthebius*, based on the aedeagal and abdominal structures. In contrast to *Ochthebius*, both genera have the abdominal sterna clothed in a combination of hydrofuge setae and stiff, erect spines.

Gymnanthelius, **new genus**

(Fig. 38, 39)

In *Gymnanthelius hieroglyphicus* (Deane), the type species of the genus *Gymnanthelius*, a specialized ESDS is present, but the components differ in several respects from those of *Ochthebius*. The postocular area near the posteroventral angle of the eye has a strongly microreticulate shelf that terminates in a spiculate secretion area (Fig. 38:z, 39:z), with exocrine pores. This spiculate margin is continuous with a transgenal ridge (Fig. 39:r). Adjacent to the spiculate secretion area are three specialized plumose secretion delivery setae (Fig. 38:a, 39:a), each with multiply-branched tips.

The genal hydrofuge (Fig. 38:t, 39:t) is strongly asperite, but the postocular area near the delivery setae is rather sparsely pubescent and smooth. Periocular pores (Fig. 38:e, 39:e) are present adjacent to the eye facets. The hypomeral antennal pocket (Fig. 38:i, 39:i) is well developed, smooth except for an antero-

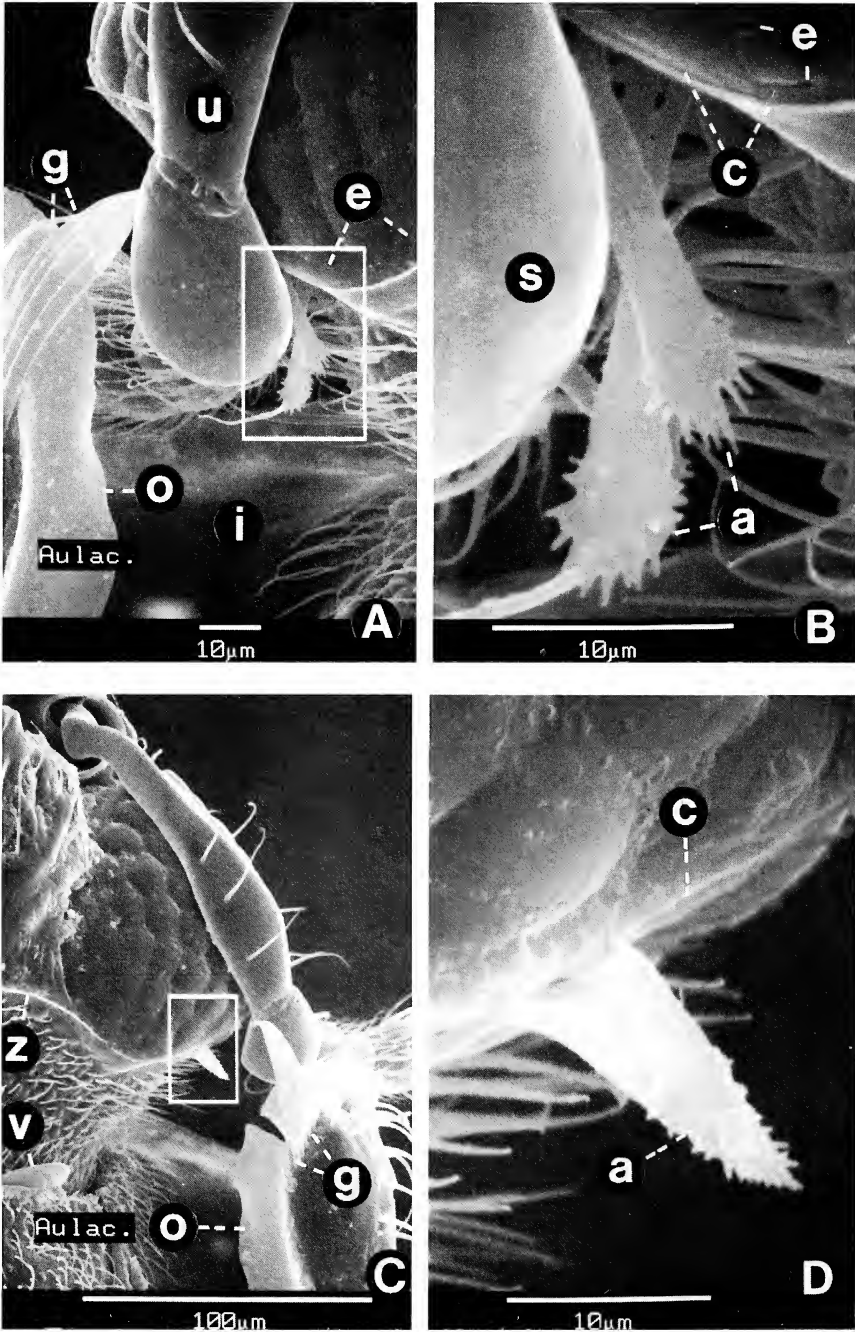


Fig. 37.—*Aulacochthebius* sp. A. Postocular and adjacent hypomeral areas. B. Rectangular area of A, enlarged. C. Venter of head and adjacent prothorax. D. Rectangular area of C, enlarged. Structures: (a) psd-setae, (c) psd-sulcus, (e) periocular exocrine pores, (g) hap-setae, (i) hypomeral antennal pocket, (o) hh-border, (s) second antennomere, (u) first antennomere, (v) cervical sclerite, (z) transgenal ridge.

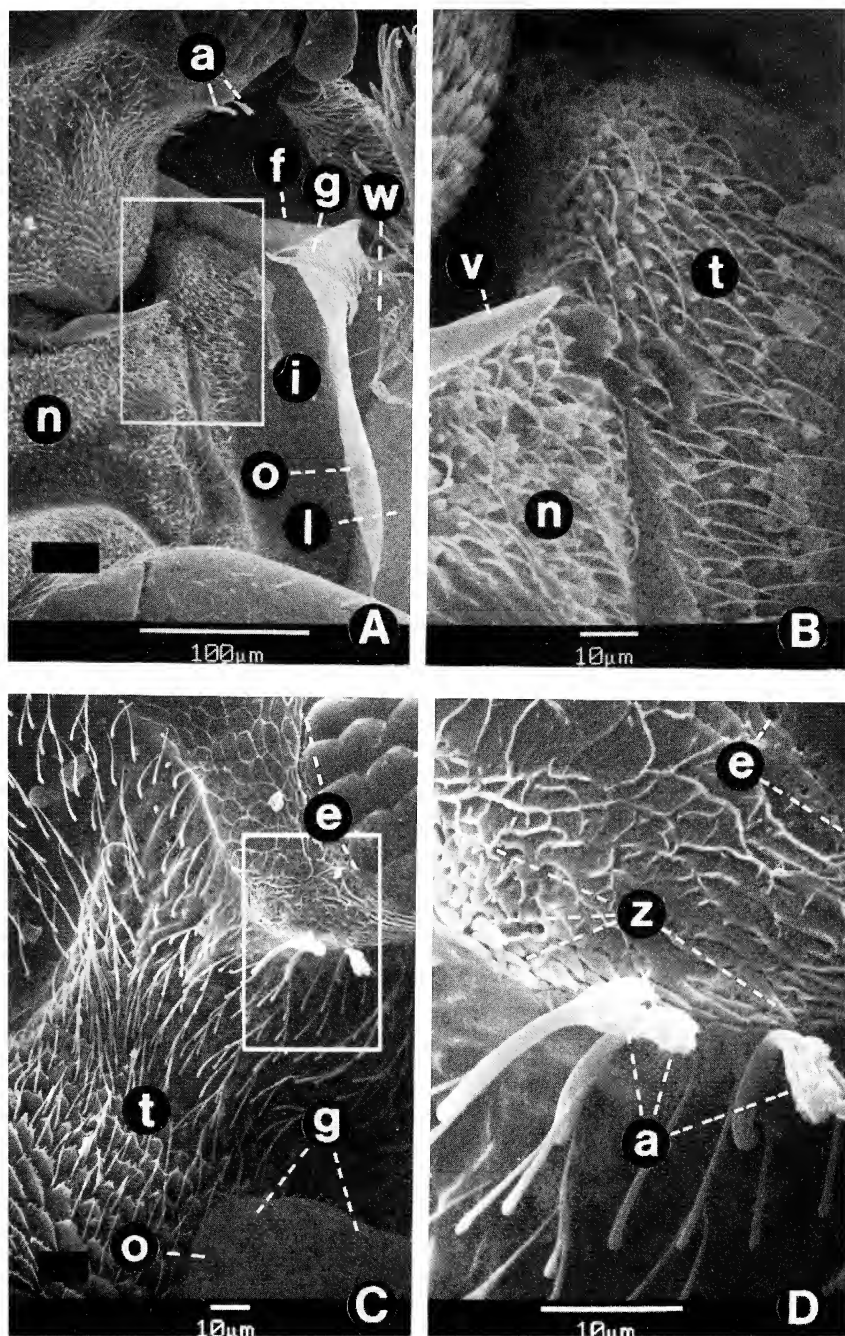


Fig. 38.—*Gymnanthelius hieroglyphicus*. A. Venter of head and prothorax, left side. B. Rectangular area of A, enlarged. C. Postocular area, posteroventral aspect. D. Rectangular area of C, enlarged. Structures: (a) psd-setae, (e) periocular exocrine pores, (f) ah-border, (g) hap-setae, (i) hypomeral antennal pocket, (l) lh-border, (n) prosternum, (o) hh-border, (t) asperite hydrofuge, (v) cervical sclerite, (w) wet-hypomeron, (z) postocular exocrine secretion distribution area.

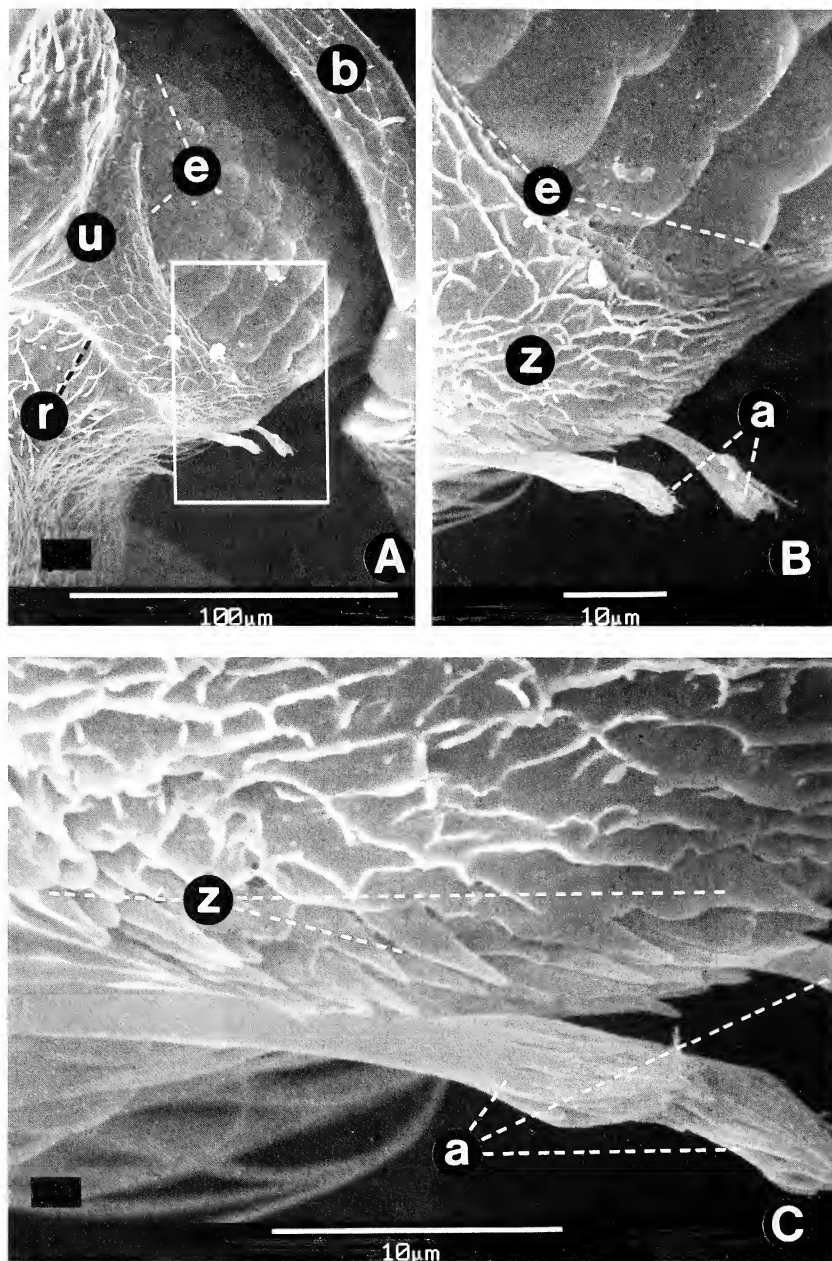


Fig. 39.—*Gymnanthelius hieroglyphicus*. A. Venter of left eye. B. Rectangular area of A, enlarged. C. Postocular exocrine secretion distribution area. Structures: (a) psd-setae, (b) first antennomere, (e) periocular exocrine pores, (r) transgenal ridge, (u) subocular antennal groove, (z) postocular exocrine secretion distribution area.

medial asperite hydrofuge area (Fig. 38:t). The hypomeral, lateral, anterior, and posterior hyaline borders are all well developed. The hypomeral antennal pocket setae (Fig. 38:g) are short (relative to those of *Ochthebius*), extending only slightly beyond the hh-border. The wet-hypomeron (Fig. 38:w) is small. The profemur has a distal cluster of strong spines.

The structures of the postocular area, especially the spiculate exocrine area, do not seem to be a condition derived from the secretion sulcus of *Ochthebius*. It is problematic whether or not the secretion delivery setae of *Gymnanthelius* are homologous with those of *Ochthebius*. A more complete description of this new genus, together with descriptions of additional species, will be presented elsewhere.

Genus *Hughleechia* Perkins (Fig. 40)

The genus *Hughleechia* is based on *H. giulianii* Perkins, an intertidal species from Australia (Perkins, 1981). The second known species of *Hughleechia*, an undescribed intertidal species from Tasmania, is similar to *giulianii* in structures of the ESDS, but quite dissimilar to that species in several other external features.

Unlike *Ochthebius*, the postocular area does not have a secretion sulcus near the posteroventral angle of the eye. There is, however, a transgenal secretion sulcus (Fig. 40:z). The cuticle is distinctively raised on each side of the sulcus to form a transgenal ridge. The secretion delivery setae (Fig. 40:a) are elongate and appear to be paired. The postocular hydrofuge (Fig. 40:t) is asperite and has exocrine pores (Fig. 40:p) near the base of the secretion delivery setae.

The hypomeral antennal pocket (Fig. 40:i) is well developed, the cuticle smooth except microreticulate medially and hydrofuge pubescent anteromedially. Exocrine pores are moderately dense in the antennal pocket. The hh-border (Fig. 40:o) is quite large anteriorly, such that it contacts the psd-setae. In its posterior part, the hh-border is quite narrow and becomes contiguous with the ph-border. The posterior border of the pronotum is arcuate such that there are no posterior angles. In *H. giulianii*, the hh-border and ah-border are not contiguous, the ah-border being absent over the area of the postocular emarginations of the pronotum (Fig. 40A). In the undescribed species, however, the two hyaline borders are contiguous. The wet-hypomeron is well developed. The lh-border is absent. The hypomeral antennal pocket setae are present, but unlike *Ochthebius*, do not extend beyond the hh-border. The profemur does not have a distal spine cluster, the spines in this area being small as are others on the profemur.

Subtribe Meropathina, new subtribe

This new subtribe comprises the genera *Meropathus* (type genus), *Tympallopatrium*, and *Tympanogaster*. Members of the subtribe have a primitive antennal pocket. The metasternum has a large glabrous area or tabella (a derived condition), except in *Meropathus* where the metasternum is greatly reduced—associated with flightlessness. All known members are south temperate (Gondwanan) in distribution.

These genera form a distinct clade based on the derived condition of the aedeagus: lacking parameres, the main-piece characteristically shaped and not strongly arcuate basally. Additionally, in males of these three genera the last abdominal sternum lacks a strut—clearly a derived condition, probably associated

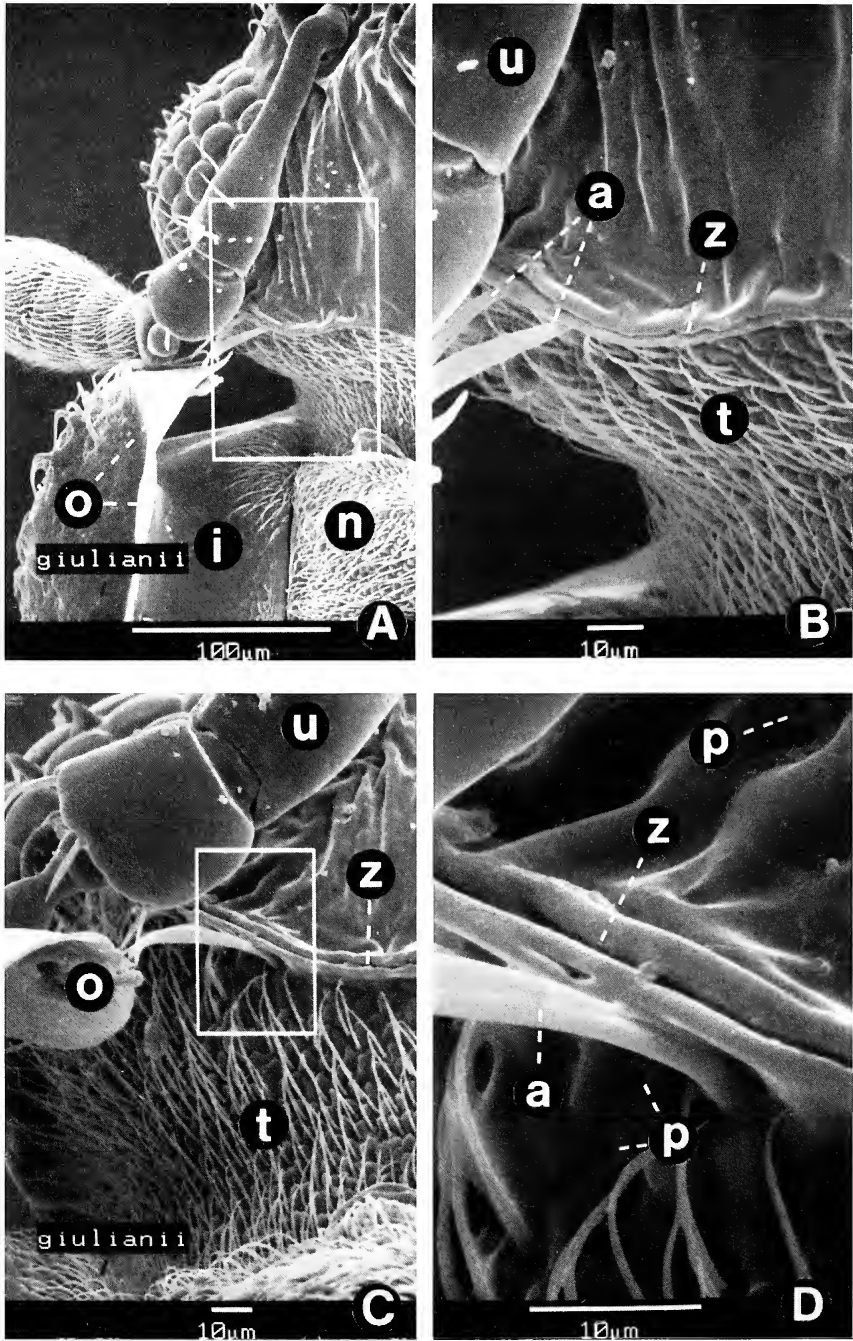


Fig. 40.—*Hughleechia giulianii*. A. Venter of head and prothorax, right side. B. Rectangular area of A, enlarged. C. Postocular area, posteroventral aspect. D. Rectangular area of C, enlarged. Structures: (a) psd-setae, (i) hypomer al antennal pocket, (n) prosternum, (o) hh-border, (p) exocrine pores, (t) postocular asperite hydrofuge, (u) first antennomere, (z) transgenal exocrine secretion sulcus.

with aedeagal morphology; all other Hydraenidae have a strut. In females the last sternum (seventh visible) is either completely concealed beneath the sixth, or with only the distal margin exposed.

Tympallopatrium and *Tympanogaster* share a distinct derived condition of the antenna: the second article is large and its distal end forms a cupule into which fits the following article and (partially so) the preclub article. The preclub article (morphological article number 6), cupuliform in most Hydraenidae, is only very marginally so (if at all) in *Meropathus*, and not at all cupuliform in *Tympallopatrium* and *Tympanogaster*.

It appears that the dorsal vestiture and sculpture morphocline in the Meropathina proceeds from a strongly setose condition, such as is present in large-bodied members of the *novicius* group of *Tympanogaster*, toward a less roughly sculptured condition, and finally to the very smooth and small-bodied members of the *deanei* group of *Tympanogaster*.

Ecologically, the Meropathina cline apparently began with fungus dwelling, proceeded to litter dwelling, then to inhabiting mossy margins of aquatic habitats such as waterfalls, and finally to mossy downstream sides of rocks and other splash-zone aquatic microhabitats. This ecocline corresponds with the morphocline of increasingly smooth dorsal sculpture.

Members of the genus *Meropathus* are discussed by Perkins (1981). The placement of some eastern Australian and Tasmanian species in *Meropathus* by Janssens (1967) and Bameul (1989) are in error; these species will be properly placed elsewhere, within the context of a generic revision.

Genus *Meropathus* Enderlein (Fig. 41)

Meropathus campbellensis Brookes, a nonaquatic species from Campbell Island, lacks components of the specialized ESDS.

The eyes of this species are reduced, but the approximate former outline of the posteroventral angle is clearly revealed by the line of periocular pores (Fig. 41:e). The postocular hydrofuge (Fig. 41:t) is well developed and of the asperite type. Exocrine pores (Fig. 41:p) are moderately dense within the hydrofuge near its anterior limit in the genal area.

The hypomer al antennal pocket (Fig. 41:h) is very weakly developed and asperite-hydrofuge, except a smooth narrow lateral margin that is wider anteriorly. The free edge of this lateral margin forms a stiff ridge that does not have a hyaline margin; this ridge is continuous with the (wider) anterior and posterior hyaline borders. The wet-hypomer on is absent. The profemor has a distal spine cluster.

Tympallopatrium, new genus (Fig. 42, 43)

Type Species.—*Tympallopatrium longitudum*, new species.

Diagnosis.—Recognized among Ochthebiinae by the eight-articled antenna (three + club) having the second article apically cupuliform, the prominent ocelli located near the eyes, the basomedial tumidity of the frons behind which are three longitudinal carinae, the transversely convex and setose dorsum, the shape of the mentum, the gular ridge, the median metasternal impression, the lack of a lateral hyaline border, and features of the antennal pocket.

Description.—**Antennal pocket**. The postocular area has a distinctive transgenal ridge (Fig. 42:r)

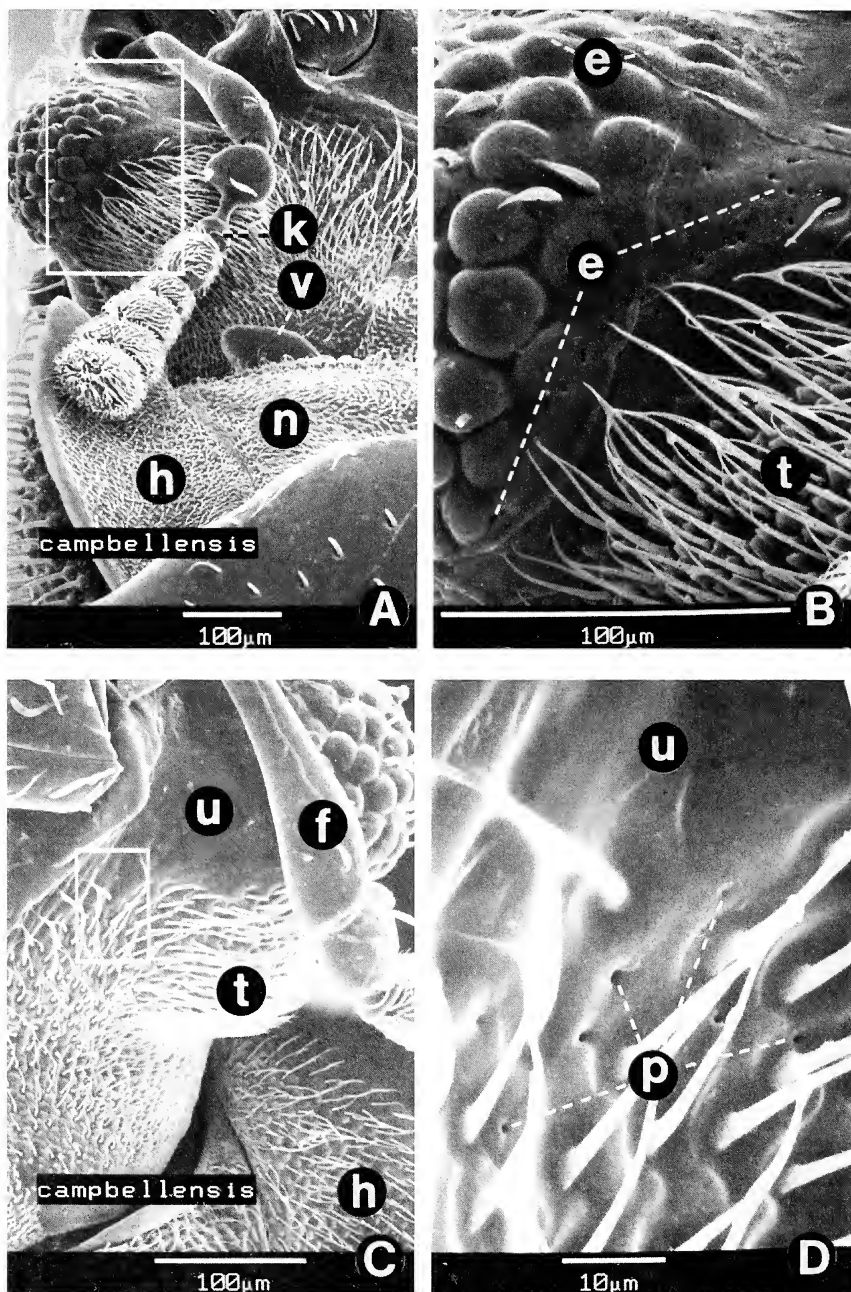


Fig. 41.—*Meropathus campbellensis*. A. Head and prothorax, posteroventral aspect of right side. B. Rectangular area of A, enlarged. C. Venter of head and prothorax, left side. D. Rectangular area of C, enlarged. Structures: (e) periocular exocrine pores, (f) first antennomere, (h) hydrofuge hypomeron, (k) cupule article of antenna, (n) prosternum, (v) cervical sclerite.

adjacent to the posteroventral angle of the eye. The postocular hydrofuge (Fig. 43:t) is moderately dense and of the asperite type, whereas the genal pubescence (hydrofuge?; Fig. 42:p, 43:p) is sparse, nonasperite, and has few exocrine pores. Periocular pores (Fig. 42:e, 43:e) are present.

The hypomeral antennal pocket is moderately well developed, the medial half hydrofuge pubescent (asperite type), the lateral half nonpubescent and weakly microreticulate (Fig. 42A:i, 43A). The lateral margin of the antennal pocket forms a ridge, but its free edge does not extend to form an hh-border; this ridge is continuous with the ah-border, but is not continuous with the ph-border. The wet-hypomeron is quite small, consisting of tuberculate enlargements upon which are placed setae. The (presumed) antennal cleaner of the prosternum is well developed (Fig. 42:a, 43B:a). The profemur has large spines over most of the upper surface; these spines are not organized to form a distal spine cluster.

Other characters. Form transversely convex. Dorsal reliefs strongly setose, including frons tumidity, ocelli, four longitudinal sinuate costae on pronotum, and four costae on elytra (on even-numbered interseries, costae often interrupted). Ocelli prominent, located next to eyes. Frons with basomedial tumidity, separated from ocelli by longitudinal sulcus; three strong parallel longitudinal carinae behind tumidity. Antennomeres eight (three + club); second cupuliform, third very small, not cupuliform. Maxillary palpi short, ochthebiine. Labrum deflexed. Mentum longer than wide. Gula with a prominent transverse ridge. Pronotum with disc transversely convex, bearing four sinuate setose costae; anterior and posterior hyaline borders narrow, bearing tiny cuticular processes; lateral margins arcuate, denticulate, and setose, lacking hyaline border, sometimes minutely excavate near posterior angles. Elytra with ten series of punctures, suture and even-numbered interseries at least in part costate and setose. Prosternum narrow in front of procoxae, with low midlongitudinal carina. Hypomeron with carina forming margin of antennal pocket. Metasternal disc shining, with median impression. Intercoxal sternite small, triangular. Legs short, tarsi very short, five–five–five. Hydrofuge pubescence present on postocular area, bubble-hypomeron, notal postcoxal projection, mesosternum, narrow band around shining metasternal area, first abdominal sternum, and narrow lateral band of abdominal sterna two to five.

Etymology.—Greek, *tympa* (from *Tympanogaster*), plus *allo* (other), plus *patrum* (country, walk): “walk to a different drummer”; gender neuter.

Tympallopattrum longitutum, new species

Type Material.—Holotype male, deposited in MCZ, and 12 paratypes with data: Western Australia, Pemberton, x.1931, P. J. Darlington, (MCZ; some to be deposited in ANIC and CMNH). Additional paratypes: M. V. “Agios Nikolaos III,” Fremantle F67 [quarantine interception], 15.x.1976, (5 ANIC). Western Australia, 48 km N Albany, Porongurup Nat. Pk., 24.xii.1976, litter under karri and Acacia at head of Bolganys Creek, FMHD #76-530, J. Kethley, (49 FMNH; some to be deposited in ANIC, CMNH, and MCZ).

Description.—Size (mm × 100; length/width): body 152/66, head 30/42, pronotum 39/54, elytra 104/66. Color brown. Labrum deflexed, wider than long, in males with small dentiform median process and basomedian fovea, in females simple. Frons and clypeus setose, more densely so laterally. Pronotal disc with anterior midlongitudinal fovea, between setose costae, distinctly longer than but only slightly wider than fovea behind it, low relief between foveae very weakly developed; punctures in anterior fovea forming two short longitudinal series; two granules at margin of each pronotal puncture. Pronotal lateral margin granulose and setose, arcuate, minutely excavate at posterior angles. Elytra nearly parallel-sided, flat on disc, with ten quite regular series of punctures; costae straight, present on even-numbered intervals as follow: second: interrupted over short distance slightly past midlength; fourth: interrupted over short distance in apical fourth, joining with second slightly before apices; sixth: ended near distal fourth; eighth: ended just before place where second and fourth become confluent. Elytral margin minutely granulate and setose. Hypomeron with antennal pockets wide, dull; wet-hypomeron very narrow, present only in posterior half. Metasternal disc shining, with nearly parallel-sided mid-longitudinal sulcus from base to anterior fourth where joins low midlongitudinal carina.

Etymology.—Latin, *longitutum* (length, longitude), a reference to longitudinal orientation.

Discussion.—A figure of the male genitalia of *T. longitutum*, and descriptions of additional new species in the genus, will be given in a separate paper.

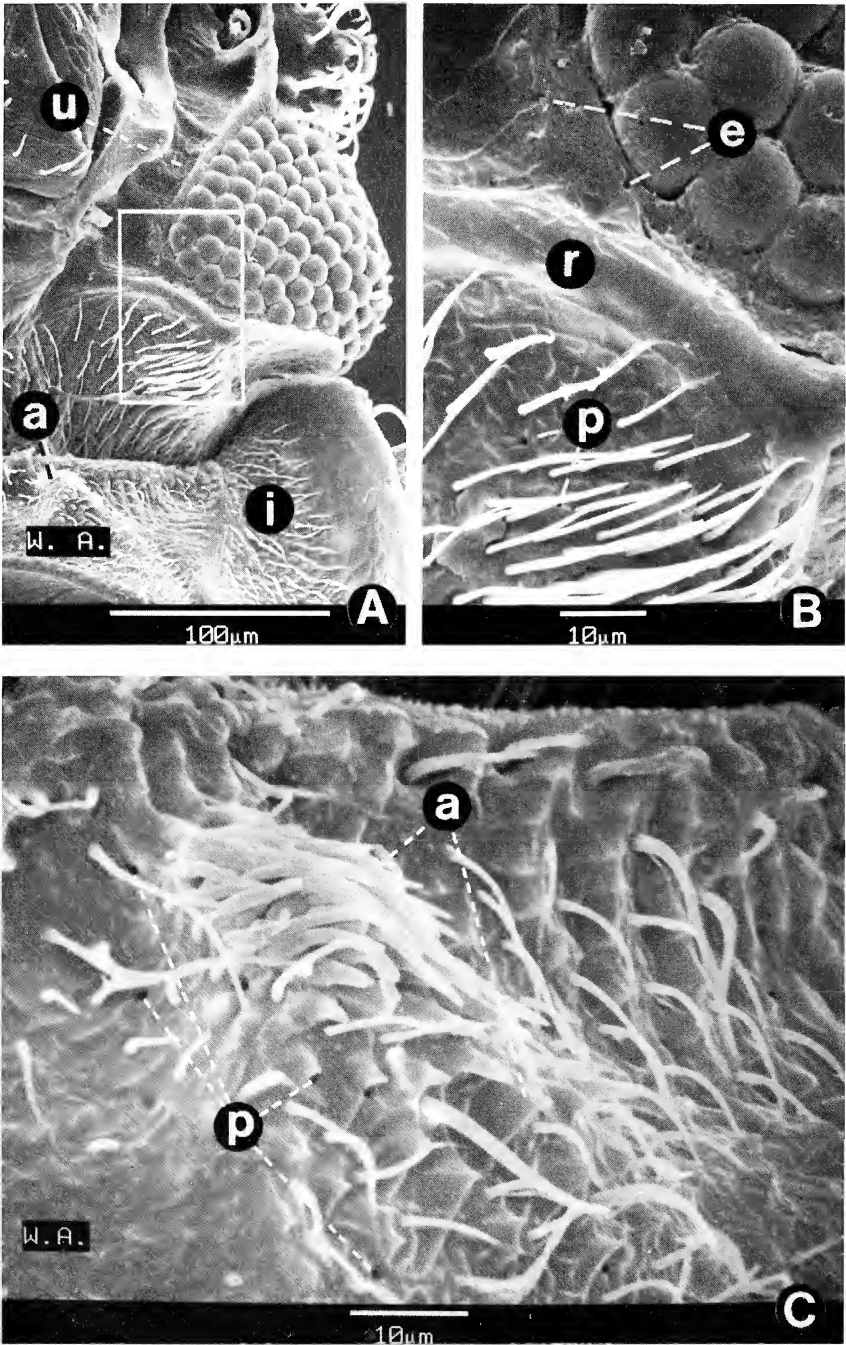


Fig. 42.—*Tympallopattrum longitudum*. A. Head and prothorax, posteroventral aspect of left side. B. Rectangular area of A, enlarged. C. Prosternum. Structures: (a) antennal cleaner, (e) periocular exocrine pores, (i) hypomer al antennal pocket, (p) exocrine pores of gena, (r) genal ridge, (u) subocular antennal groove.

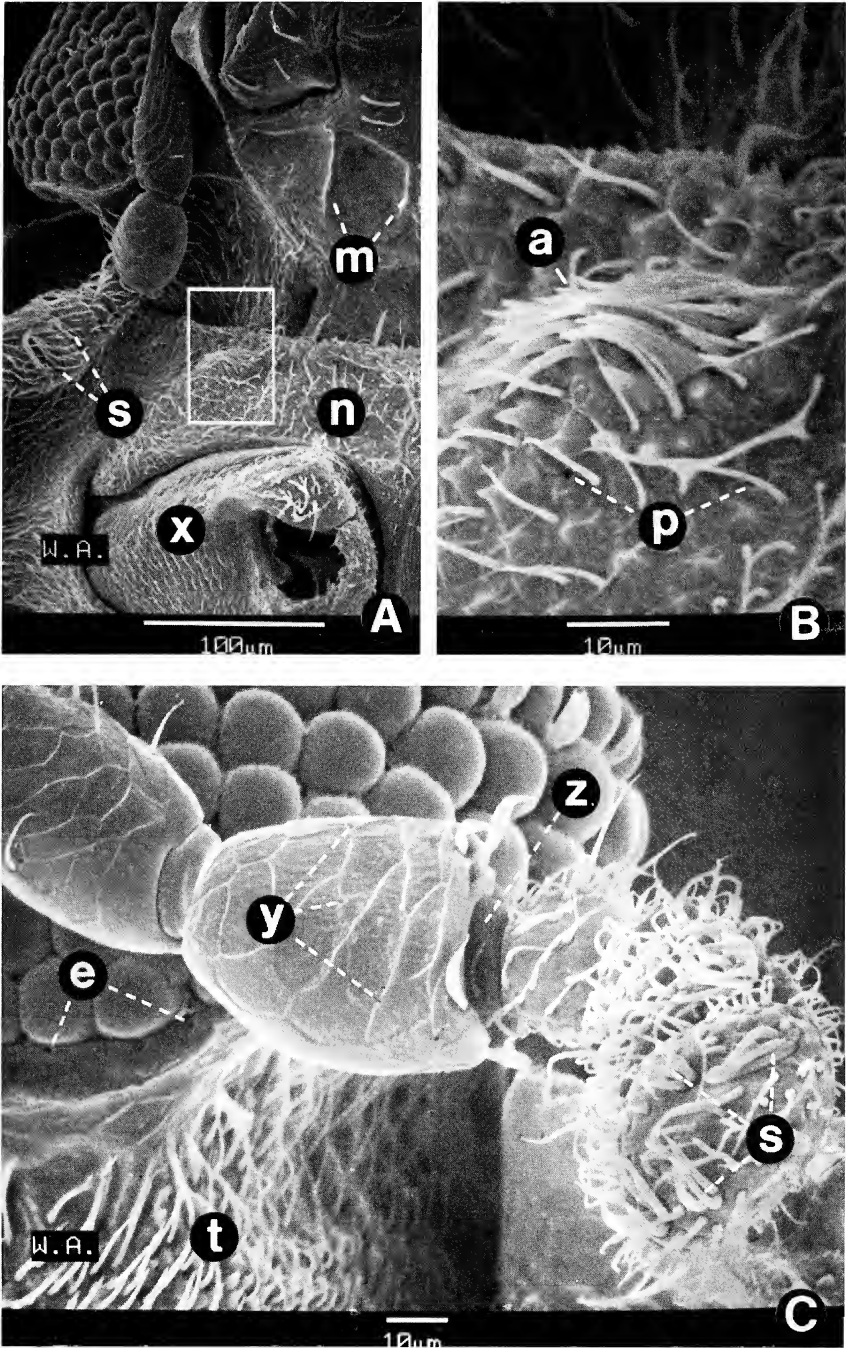


Fig. 43.—*Tympallopattrum longitudum*. A. Venter of head and prothorax, right side. B. Rectangular area of A, enlarged. C. Antenna and adjacent postocular area. Structures: (a) antennal cleaner, (e) periocular exocrine pores, (m) submental ridges, (n) prosternum, (p) exocrine pores, (s) sensilla of antennal club, (t) postocular asperite hydrofuge, (x) prococxa, (y) exocrine pores of second antennomere, (z) third antennomere.

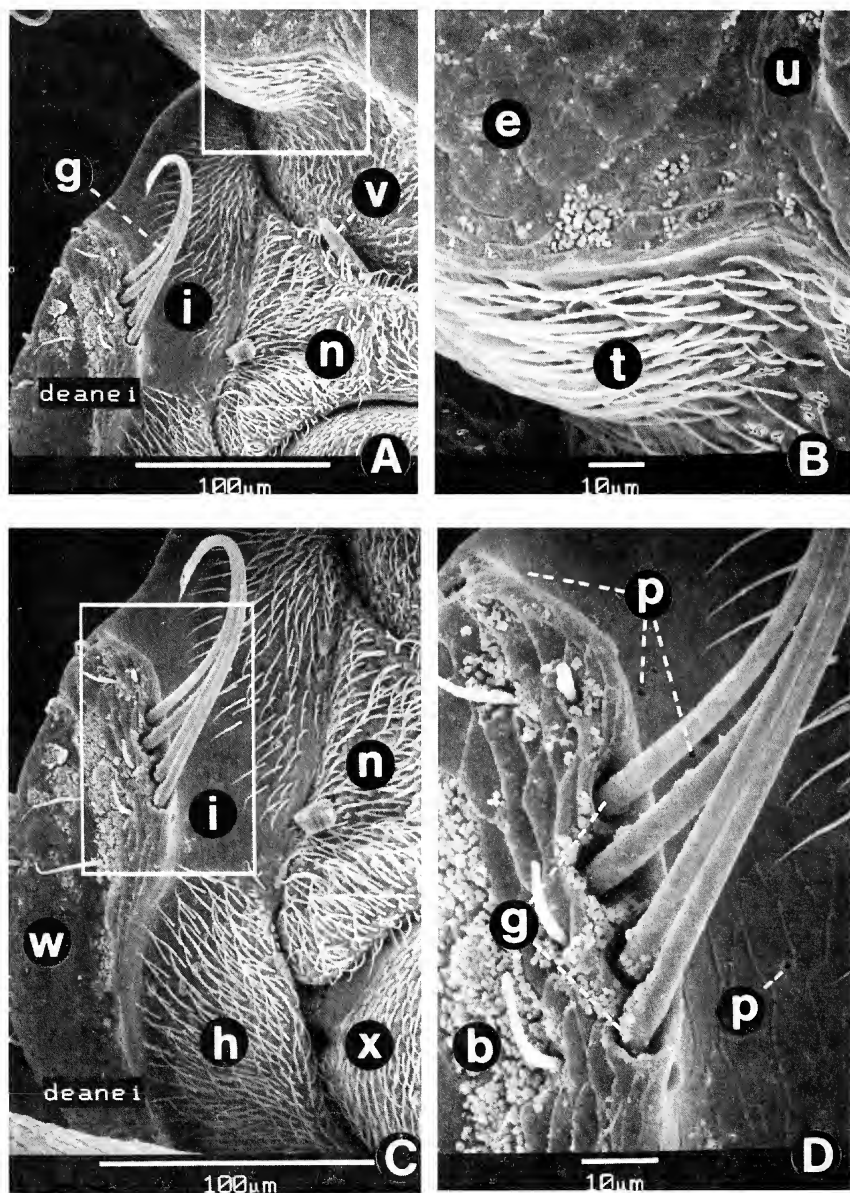


Fig. 44.—*Tympanogaster deanei*. A. Postocular and adjacent prothoracic areas, right side. B. Rectangular area of B, enlarged. C. Venter of prothorax, right side. D. Rectangular area of C, enlarged. Structures: (b) bacteria(?), (g) hap-setae, (h) hydrofuge hypomeron, (i) hypomeral antennal pocket, (n) prosternum, (p) exocrine pores of antennal pocket, (t) postocular hydrofuge, (u) subocular antennal groove, (v) cervical sclerite, (w) wet-hypomeron, (x) procoxa.

Tympanogaster Janssens
(Fig. 44, 45)

Discussion.—Members of *Tympanogaster*, an Australian and Tasmanian genus, lack a specialized ESDS. Representatives of two distinct species groups were

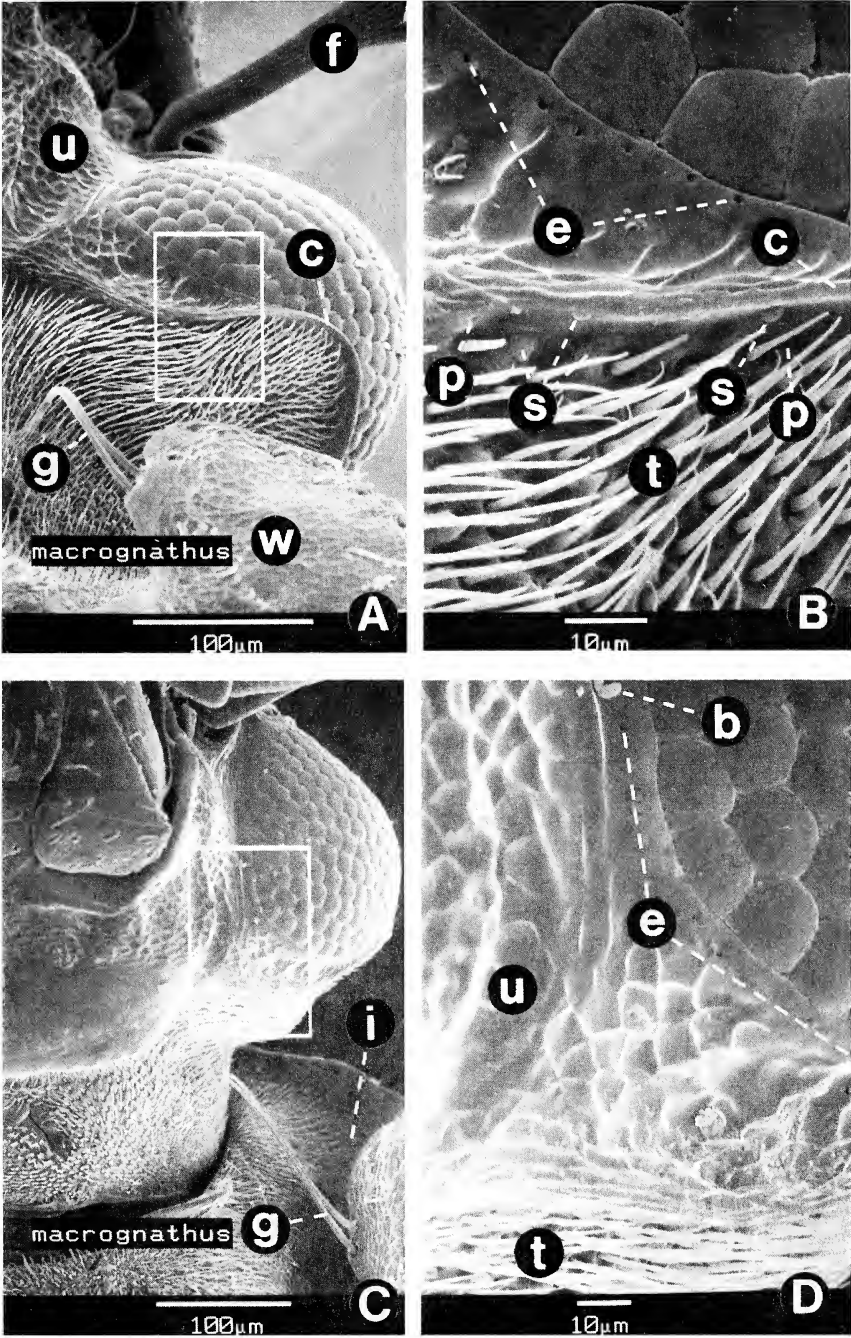


Fig. 45.—*Tympanogaster macrognathus*. A. Postocular and adjacent prothoracic areas, posteroventral aspect of left side. B. Rectangular area of A, enlarged. C. Ventral aspect of head and adjacent prothorax, left side. D. Rectangular area of C, enlarged. Structures: (b) bacteria(?), (c) postocular carina, (e) periocular exocrine pores, (f) first antennomere, (g) hap-setae, (i) hypomeral antennal pocket, (p) exocrine pores, (s) presumed exocrine secretion, (t) postocular hydrofuge, (u) subocular antennal groove, (w) wet-hypomeron.

studied, *T. deanei* Perkins (*deanei* group) and *T. macrognathus* (Lea) (*macrognathus* group). Members of the *macrognathus* group have been incorrectly placed in the genus *Meropathus* by Janssens (1967) and Bameul (1989). This genus is currently being revised by the author; additional study is needed to determine if a new genus is warranted for the *macrognathus* group.

Description.—**Antennal pocket.** The postocular area has a distinct transgenal ridge that is a continuation of an orbital ridge (Fig. 44B:c, 45:c). The postocular hydrofuge is short and dense (asperite type; Fig. 44:t, 45:t), with sparse exocrine pores near the orbital ridge (Fig. 45:p), and presumed exocrine secretions (Fig. 45:s). Periocular pores are present (Fig. 45:e).

The hypomer al antennal pocket (Fig. 44:i, 45:i) is well developed. In *T. macrognathus* it has a smooth, nonpubescent surface, except for the anteromedial area that is hydrofuge pubescent (Fig. 45C), whereas in *T. deanei* the pocket is hydrofuge pubescent over about the medial half (Fig. 44C), the remainder being nonpubescent, weakly microreticulate, and having sparse exocrine pores (Fig. 44D:p).

The hypomer al antennal pocket setae (Fig. 44:g, 45:g) differ in the two species groups, consisting of two setae in the *macrognathus* group (Fig. 45) and four in the *deanei* group (Fig. 44). The wet-hypomer on (Fig. 44:w, 45:w) is large, and separated from the bubble-hypomer on by a well-developed hypomer al carina.

The hh-border and lh-border are absent. The ah-border, when present, is extremely narrow; in some specimens it is absent, perhaps abraded away by movements of the head (e.g., Fig. 45C). The ph-border, when present, is extremely narrow and limited to about the middle quarter of the base; in some specimens it is absent. The profemur is armed with spines on the upper, distal surface, but these spines are very short, about the same length as other spines on the profemur, and are not organized into a discrete distal spine cluster.

Subtribe *Neochthebina*, new subtribe

This monotypic subtribe is erected for the genus *Neochthebius*. The postocular area and hypomer on are plesiomorphic, and hyaline borders are absent. The antenna has the derived condition, relative to the *Meropathina*, of a cupuliform preclub (anatomical fourth) article.

Neochthebius Orchymont

(Fig. 46, 47)

Neochthebius vandykei (Knisch), an intertidal species from western North America, lacks all components of the specialized exocrine secretion delivery system. The absence of the specialized ESDS components corroborates the elevation of *Neochthebius* from subgeneric to generic status (Perkins, 1981).

The postocular area has well-developed periocular pores (Fig. 46:e, 47:e). The periocular pore area at the posteroventral angle of the eye is comparatively wide and the adjacent facets are comparatively flattened, both conditions reflecting the reduced eye size. The postocular hydrofuge area is of the asperite type, and has sparse exocrine pores (Fig. 46:p, 47:p).

The hypomer al antennal pocket (Fig. 46:i, 47:i) is moderately developed, microreticulate throughout (no smooth lateral band), and lacks hydrofuge pubescence except for a small patch of setae at the anteromedial extreme. The hh-border and lh-border are entirely absent, whereas the ah-border and ph-border are present. The profemur lacks a distal spine cluster.

Subtribe *Protochthebiina*, new subtribe

This subtribe is erected for the genus *Protochthebius*. The postocular area in this subtribe is plesiomorphic, and the hypomer on has a hypomer al hyaline border with horizontal (plesiomorphic) orientation, but lacks a lateral hyaline border.

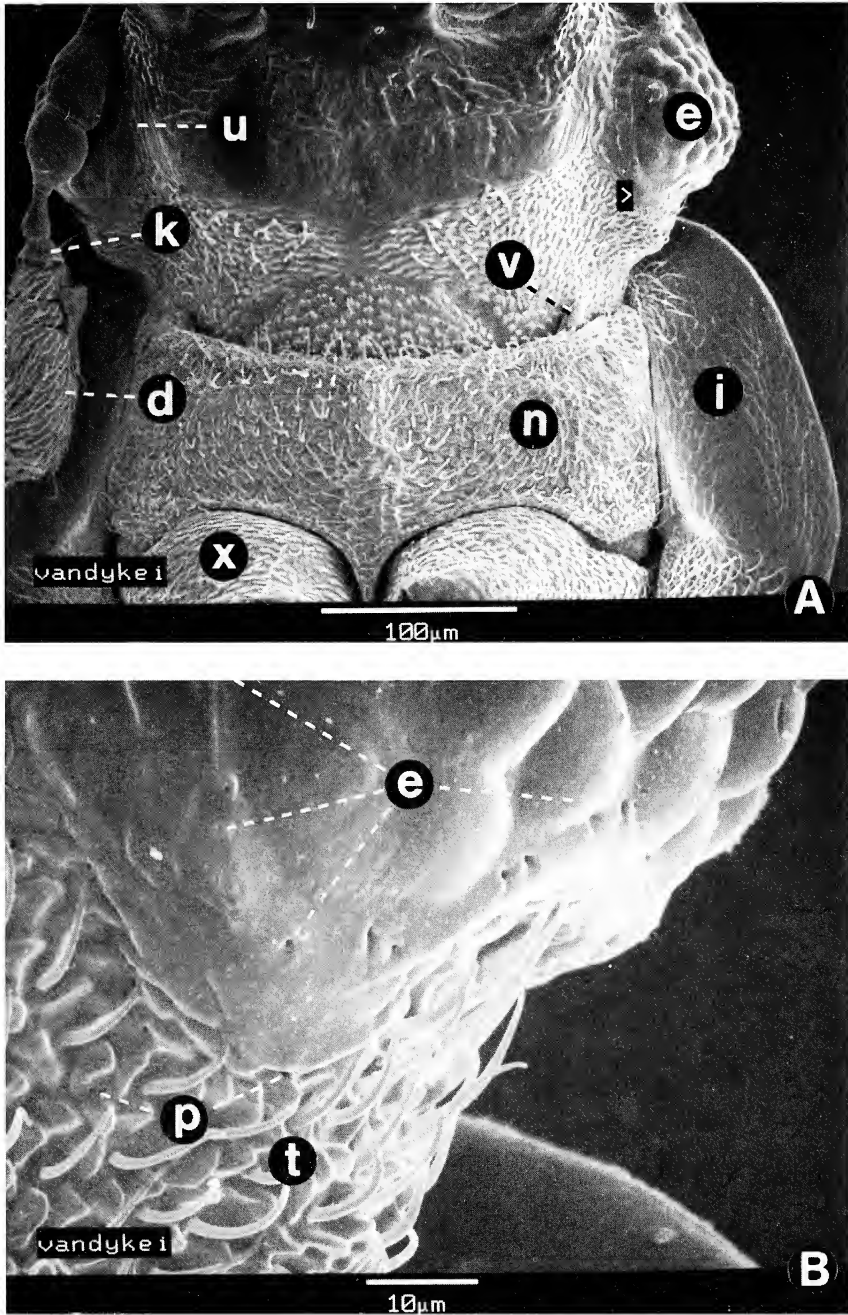


Fig. 46.—*Neochthebius vandykei*. A. Venter of head and prothorax. B. Postocular area. Structures: (d) antennal club, (e) eye and periocular exocrine pores, (i) hypomerall antennal pocket, (k) cupule article of antenna, (n) prosternum, (p) exocrine pores, (t) postocular asperite hydrofuge, (u) subocular antennal groove, (v) cervical sclerite, (x) prococxa.

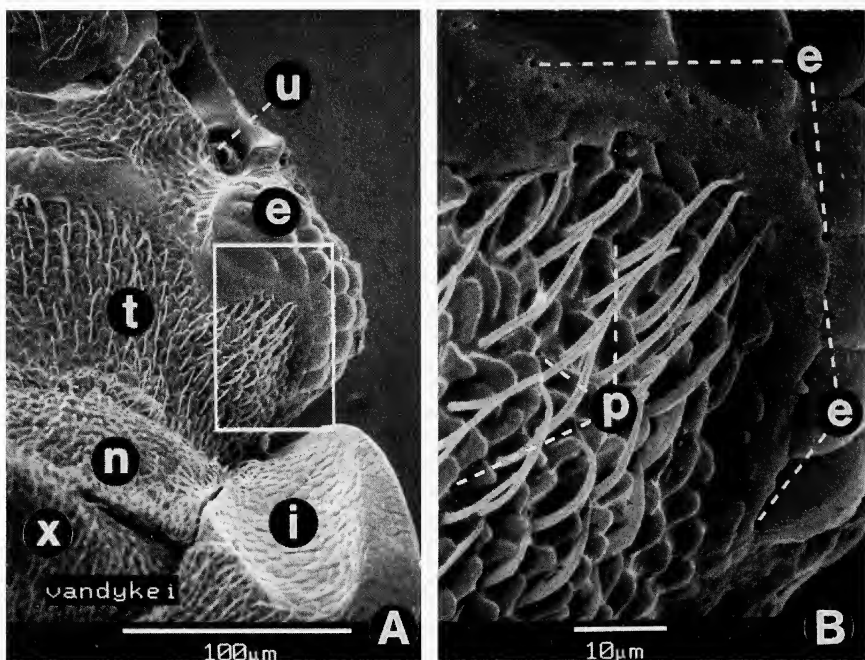


Fig. 47.—*Neochthebius vandykei*. A. Head and thorax, posteroventral aspect of left side. B. Rectangular area of A, enlarged. Structures: (e) eye and periocular exocrine pores, (i) hypomer al antennal pocket, (n) prosternum, (p) exocrine pores of postocular asperite hydrofuge, (t) genal asperite hydrofuge, (x) procoxa.

Protochthebius, new genus
(Fig. 48, 49)

Type Species.—*Protochthebius satōi*, new species.

Diagnosis.—Recognized among Ochthebiini by the nine-articled antenna (four + club) having the second article oval, the third slender and elongate, length subequal to combined lengths of the first three articles of the club, the fourth article cupuliform; the postocular area lacking secretion distribution setae; the antennal pockets of the hypomer on microreticulate and pubescent; the hypomer al hyaline border located at the lateral margin of the hypomer on (wet-hypomer on absent), in a horizontal plane and visible dorsally at posterior sides of pronotum; and the lateral hyaline border absent.

Description.—**Antennal pocket**. The postocular area near the posteroventral angle of the eye lacks secretion delivery setae and also lacks the associated secretion sulcus. There is, however, a transgenal sulcus (Fig. 48:c), perhaps with exocrine pores. This sulcus may represent the primitive condition from which were derived the various forms of secretory sulcus seen in *Ochthebius*, *Gymnochthebius*, *Aulacochthebius*, and *Hughleechia*. The periocular pores (Fig. 48:e) are well developed and the postocular hydrofuge (Fig. 48:t, 49:t) is dense and of the asperite type.

The prothoracic hypomer on has a very shallow antennal pocket that is entirely hydrofuge pubescent. The pubescence is borne on a microreticulate surface of distinctive pattern (Fig. 48:i, 49:i). Interspersed in this microreticulate pattern are exocrine pores. The hypomer al antennal pocket is margined laterally with a smooth border that, at its lateral extreme, becomes the hh-border (Fig. 48:o, 49:o). The hh-border is approximately in a horizontal plane, and becomes wide enough posteriorly to be seen in dorsal aspect. The hh-border is contiguous anteriorly and posteriorly with the ah-border and ph-border, respectively.

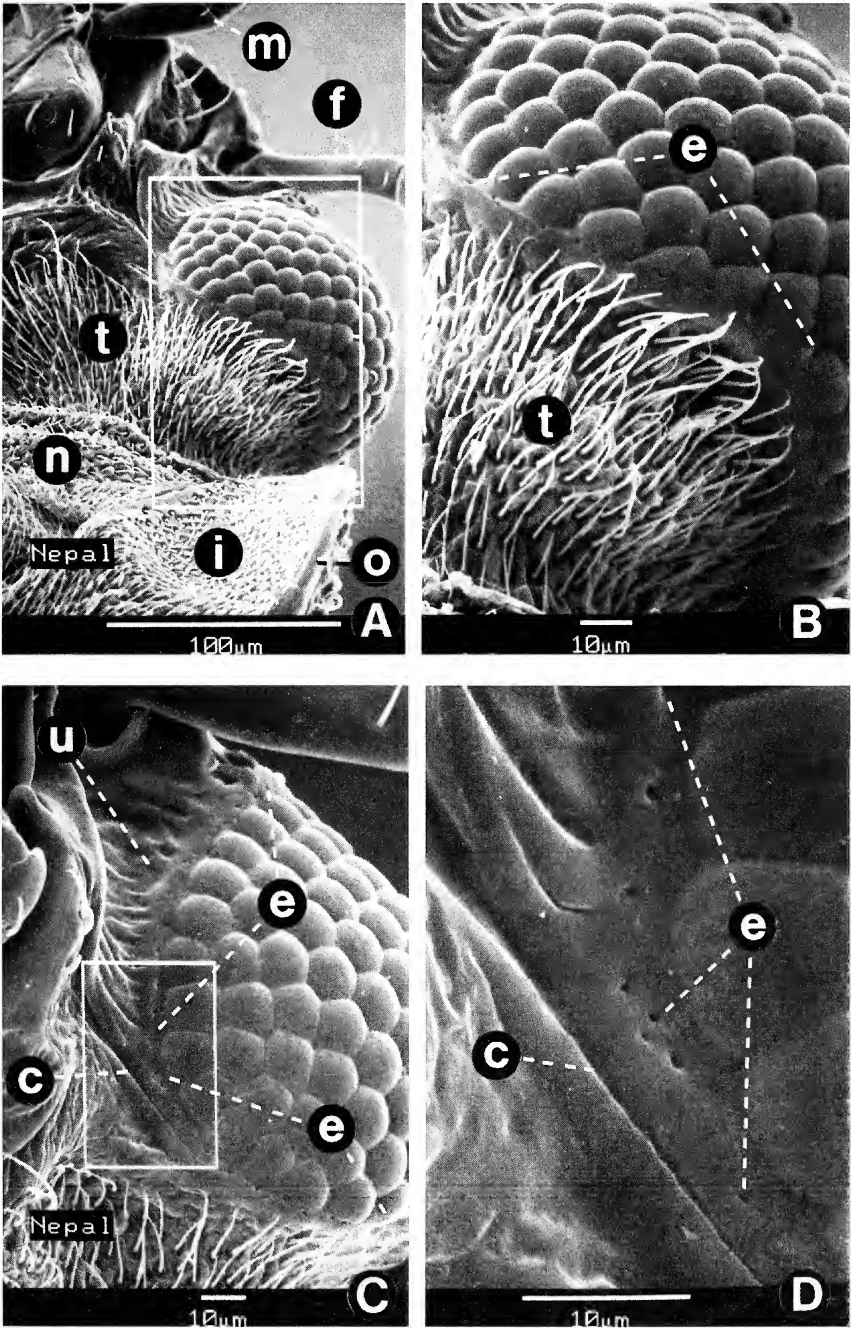


Fig. 48.—*Protochthebius satôï*. A. Head and prothorax, posteroventral aspect of left side. B. Rectangular area of A, enlarged. C. Periocular area, ventral aspect. D. Rectangular area of C, enlarged. Structures: (c) subocular secretion sulcus, (e) periocular exocrine pores, (f) first antennomere, (i) hypomer al antennal pocket, (m) maxillary palpus, (n) prosternum, (o) hh-border, (u) subocular antennal groove.

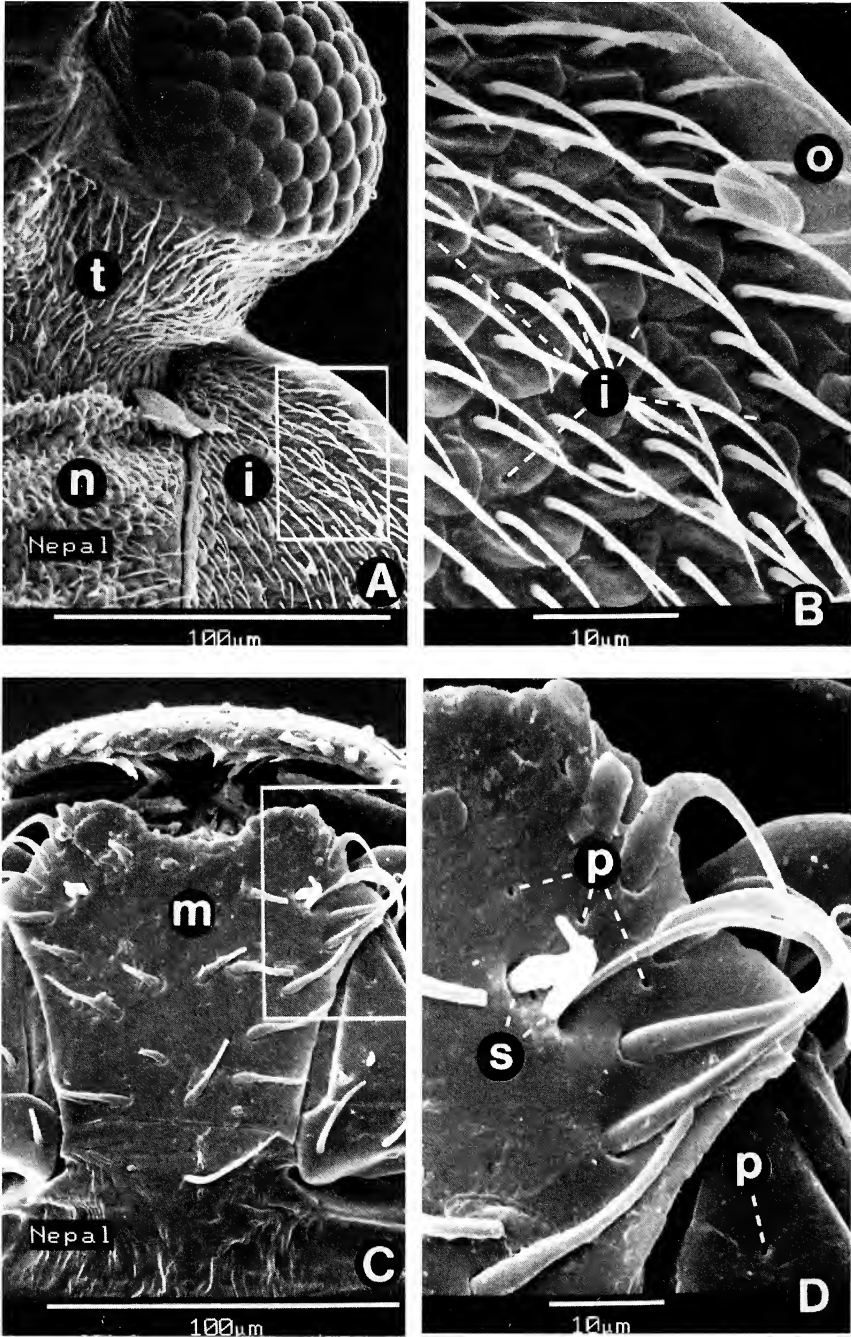


Fig. 49.—*Protocthebius satōi*. A. Venter of head and prothorax, left side. B. Rectangular area of A, enlarged. C. Mentum. D. Rectangular area of C, enlarged. Structures: (i) hypomerall antennal pocket and exocrine pores, (m) mentum, (n) prosternum, (o) hh-border, (p) exocrine pores, (s) mental sensilla, (t) genal hydrofuge.

The wet-hypomeron is absent (the hh-border being located at the lateral extreme of the hypomeron). An lh-border is absent. However, the prothorax is narrowed at the base, and in dorsal aspect the hh-border is visible in this area, and can be misinterpreted as the lh-border. The profemur does not have a distal spine cluster.

Other characters. Size small, about 1.22 mm long, form moderately elongate, moderately transversely convex. Dorsal setae weakly developed. Ocelli located near eyes. Antennomeres nine (four + club); second oval, third slender and elongate, length subequal to combined lengths of first three articles of club, fourth article cupuliform. Maxillary palpi short, length ratios of articles two to four as one : four : one, third article twice width of fourth (last). Labrum moderately deflexed from plane of clypeus. Pronotal disc with midlongitudinal sulcus and two admedian foveae on each side; lateral depressions well developed. Anterior and posterior hyaline borders narrow. Elytra with ten series of punctures. Prosternum and procoxae about equal in length. Antennal pockets of hypomeron wide, shallow, microreticulate, and pubescent. Hypomeral hyaline border positioned laterally (wet-hypomeron absent), in horizontal plane, visible dorsally at posterior sides of pronotum; lateral hyaline border absent. Metasternal disc moderately convex, lacking impressions. Intercoxal sternite small, triangular. Legs short, tarsi short, five–five–five. Hydrofuge pubescence present on postocular area, hypomeron, notal postcoxal projection, mesosternum, metasternum, and first five visible abdominal sterna.

Etymology.—Greek, *proto* (first), plus *Ochthebius*; gender masculine.

Protochthebius satô, new species

Type Material.—Holotype male: Nepal, Sindhu, Lamosangu, 900m, 18–21.x.1979, M. Satô leg.; deposited in NSMT. Forty-five paratypes with same data as holotype; deposited in CMNH, FMNH, MCZ, and MSC.

Description.—Size (mm × 100; length/width): body 122/53, head 27/33, pronotum 27/39, elytra 78/53. Color black, antennae brown. Dorsum entirely dull, with dense micropunctulate ground sculpture plus, on frons and pronotum, larger secondary punctation giving subrugulose surface. Labrum wider than long, apicomediaally emarginate in both sexes. Frons with two well-developed foveae. Pronotal disc with midlongitudinal sulcus that is shallowest in the middle, giving the impression of two foveae, one behind the other; two foveae on each side of sulcus, one behind the other, the posterior nearly twice as large as the anterior; lateral depressions well developed. Pronotal lateral margins strongly arcuate before middle, constricted behind, where is visible hypomeral hyaline border. Elytra transversely convex, longitudinally flat on disc, with ten very regular series of relatively large punctures, slightly larger than width of intervals, and closely spaced longitudinally, each puncture with a minute seta; intervals very slightly rounded. Elytral margin narrowly explanate. Metasternal disc dull, entirely microreticulate, and hydrofuge pubescent.

Etymology.—I am pleased to dedicate this new species to Masataka Satô, fellow aquatic coleopterist who collected the type series.

Discussion.—A figure of the male genitalia of *P. satô*, and descriptions of additional new species in the genus, will be given in a separate paper.

Subtribe Enicocerina, new subtribe

This subtribe is erected for *Enicocerus* Stephens. The postocular area has a secretion shelf, behind which are short brush-like secretion distribution setae that can be contacted by the wide anterior extreme of the hypomeral hyaline border. The hap-setae are short compared to the width of the hypomeral hyaline border. The prothorax has anterior, posterior, hypomeral, and lateral hyaline borders.

Enicocerus Stephens, new status (Fig. 50; 51A, B)

Discussion.—The following description is based on SEM and transparency mounts of *E. exsculptus* and transparency mounts of *E. benefossus*.

Description.—**Antennal pocket.** The postocular pores are located in the same area as those of *Ochthebius* (at the posteroventral angle of the eye) but instead of being in a secretion sulcus the pores are distributed on a smooth area, the postocular secretion shelf (Fig. 50:p).

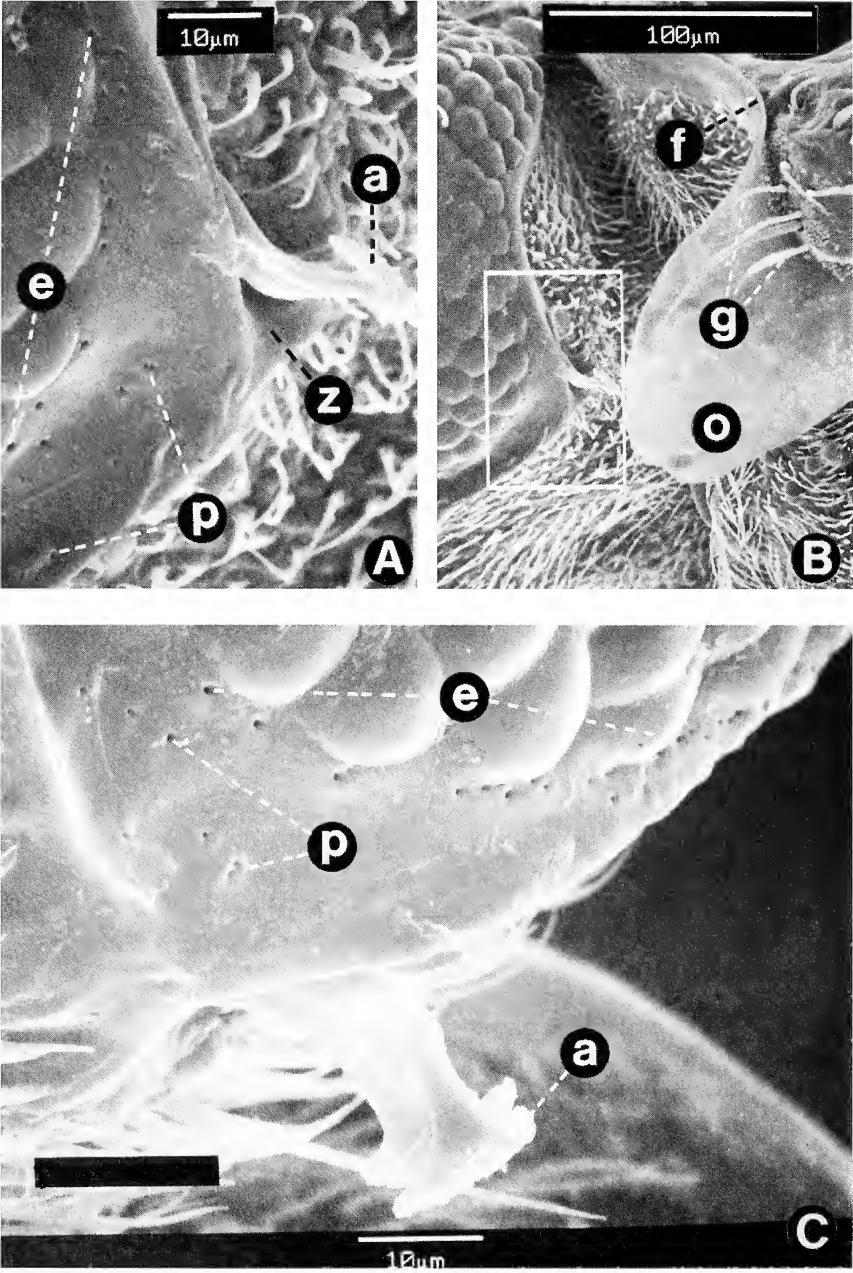


Fig. 50.—*Enicocerus exsculptus*. A. Rectangular area of B, enlarged. B. Postocular and adjacent prothoracic areas, lateral aspect. C. Postocular exocrine pore area. Structures: (a) psd-setae, (e) pericrine exocrine pores, (f) ah-border, (g) hap-setae, (o) hh-border, (p) pores on postocular exocrine secretion distribution surface, (z) cuticular ridge.

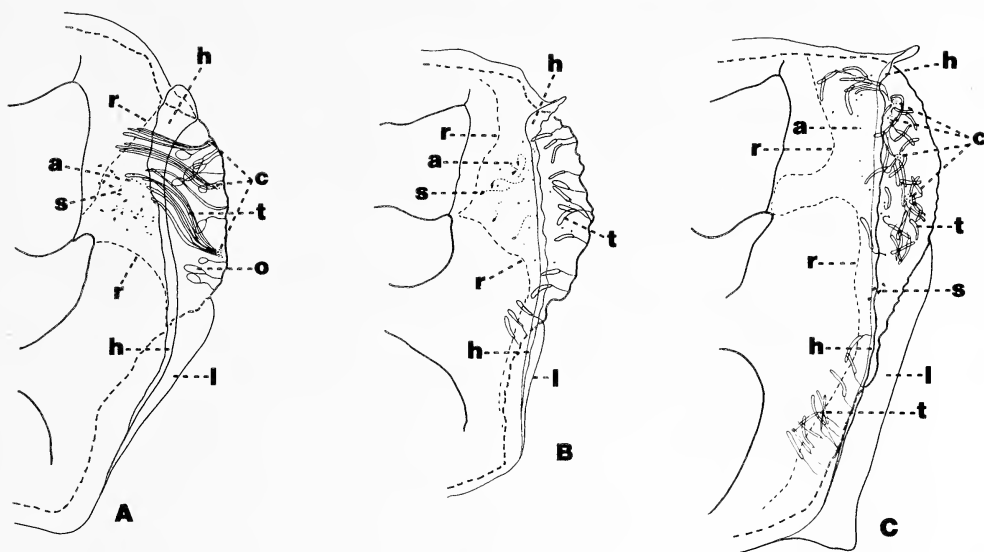


Fig. 51.—Ventral aspect of prothorax, left side, showing three types of internal end-apparatus, exocrine pore locations, and hyaline borders (setae omitted). A. *Enicocerus exsculptus*. B. *E. benefossus*. C. *Gymnochthebius plesiotypus*. Structures: (a) single exocrine pores of antennal pocket, (c) exocrine pore clusters on wet-hypomeron, (h) hh-border, (l) lh-border, (o) sacoid end-apparatus, (r) lateral limit of hypomeral hydrofuge setae, (s) spermoid end-apparatus, (t) tubuloid end-apparatus.

The psd-setae, instead of long and tapering as in *Ochthebius*, are short and expanded apically to form stout brush-like tips (Fig. 50:a). These specialized setae are supported at their bases by a cuticular ridge (Fig. 50:z). The periocular pores are well developed (Fig. 50:e). The postocular hydrofuge is short, dense, and asperite.

The hypomeral antennal pocket is well developed, hydrofuge pubescent anteromedially. The hh-border is large at its anterior extreme and the hypomeral antennal pocket setae are relatively short (Fig. 50:o, g). Consequently, the hh-border and not the pocket setae would be in a position to contact the postocular setae, a condition opposite that of *Ochthebius*. The ah-border and hh-border are contiguous (Fig. 50:f). The lh-border is well developed, contiguous with the ph-border, and across its ventral surface passes the hh-border. The profemur has a distal spine cluster, the spines of moderate length.

The hypomeral exocrine glands of *E. exsculptus* (Fig. 51A) are well developed and comprise three types, based on shape of the end-apparatus: (1) spermoid—sperm-shaped (similar to those in Fig. 3), with long ductules relative to the size of the end-apparatus (Fig. 51:s); the pores (Fig. 51:a) for these glands are solitary, and are present principally in the nonhydrofuge pubescent part of the hypomeral antennal pocket; (2) “tubuloid”—tubule-shaped, with short ductules relative to the length of the end-apparatus (Fig. 51:t); the pores of the majority of these glands are grouped into three distinct clusters (Fig. 51:c) on the wet-hypomeron, each cluster comprised of about eight pores; and (3) “sacoid”—oval or sack-shaped (Fig. 51:o), with moderately long ductules; the pores of these glands are located at or near the lateral margin of the hypomeron.

The hypomeral exocrine glands of *E. benefossus* (Fig. 51B) are much smaller than those of *E. exsculptus*. The elongate tubuloid glands of the wet-hypomeron are absent, and the glands occupying the homologous position of the sacoid glands of *exsculptus* are more tubuloid than sacoid (Fig. 51:t).

Subfamily Hydraeninae Mulsant Tribe Hydraenini

This tribe comprises the genera *Hydraena* and *Adelphydraena*. This group, elevated from subtribal level, is characterized by the following (see also Perkins, 1989): (1) the prosternal intercoxal process is expanded laterally behind the procoxae, closing the procoxal cavities (tip of each lateral process fitting into small

notch in corresponding postcoxal pronotal projection); (2) the second article of the maxillary palpus is elongate and slender; and (3) the last sternum in females has a pair of sensory clusters.

Genus *Hydraena* Kugelann

The following derived characters were given by Perkins (1989) as diagnostic for *Hydraena*: (1) mandible-labrum with interlocking structure, (2) mentum with apicomedial projection, (3) hypomeron (= proepisternum) with antennal pocket opening ventrally, and (4) antenna with nine articles. To this list can now be added the presence of the following derived characters: (1) hsd-sulcus, (2) hsd-surface, (3) dome-shaped sensilla of hypomeron, (4) gap-setae, and (5) antennal cleaner.

Subgenera of *Hydraena*

There is correspondence in the polarity of seven hypomeral morphoclines in *Hydraena*. The stepwise progression of each morphocline is represented, from ancestral to derived, by conditions present in *H. (Haenydra) gracilis* (Fig. 9A, 13A, 14A), *H. (sensu stricto) riparia* (Fig. 11A, 12), and *H. (sensu stricto) americana* (Fig. 11B, 13B, 14B). Most of these morphoclines are related to the formation and integration of the component parts of the antennal pocket.

The morphoclines involve: (1) the width of the ventral opening of the antennal pocket, (2) the locations of the hypomeral antennal pocket (hap-) setae, (3) the contact point of the hypomeral carina and the margin of the antennal pocket, (4) the degree of integration of the antennal cleaner spines, (5) the shape of the hypomeral carina, (6) the lengths of the ductules of the exocrine glands that supply the hsd-sulcus, and (7) the width and sinuosity of the hsd-sulcus.

Width of the Ventral Opening of the Antennal Pocket.—A ventrally closed antennal pocket is plesiomorphic, based on the structure of *Adelphydraena* (Fig. 52C), and other less derived genera such as *Parhydraenida*. The ventral opening, a synapomorphic character of *Hydraena* (Perkins, 1989:453), is narrowest in *gracilis* (*Haenydra*), wider in *riparia*, and wider yet in the majority of *Hydraena* (*sensu stricto*; both temperate and tropical).

Locations of the Hypomeral Antennal Pocket Setae.—The morphocline is: (a) present as a row of setae on the wet-hypomeron, as in *gracilis*; (b) some setae located on the anterior part of the antennal pocket (the most medial usually located on the hypomeral carina), as in *riparia*; and finally (c) the hap-setae forming a row along the margin of the antennal pocket, as in many *Hydraena* (both temperate and tropical).

Contact Point of the Hypomeral Carina and the Margin of the Antennal Pocket.—The morphocline is: (a) near the anterior extreme of the antennal pocket, as in *gracilis*; (b) slightly more posterior, as in *riparia*; and finally (c) adjacent to the antennal pocket, such that hydrofuge pubescence (abundant in this location in *gracilis*, and less so in *riparia*) is absent, as in many temperate and tropical species.

Degree of Integration of the Antennal Cleaner Spines.—The antennal cleaner morphocline proceeds from the relatively short-spined and less clustered cleaner of *gracilis* (Fig. 17C, D), to the longer-spined but not densely clustered condition of *riparia* (Fig. 16C), to the long-spined and densely clustered condition of most *Hydraena* (*sensu stricto*; Fig. 15A, B; 16D, 17A, B).

Shape of the Hypomerai Secretion Delivery Surface.—Primitively, as in *gracilis* (Fig. 13A, 14A), the hsd-surface is flat, very smooth, and relatively wide on each side of the hsd-sulcus; in *riparia* (Fig. 12A) the part of the hsd-surface that is medial to the hsd-sulcus is very narrow relative to the lateral part, which is slightly convex; and finally, in many species, the secretion-spreading surface is very convex and relatively narrow (e.g., Fig. 19A).

Lengths of the Ductules of the Exocrine Glands that Supply the HSD-Sulcus.—In the primitive condition, as in *gracilis* (Fig. 10A:f), the end-apparatus is relatively small and located immediately below the exocrine pores. In the intermediate condition, as in *riparia* (Fig. 11A:f), the end-apparatus is larger and slightly farther from the pores. In the most derived condition, as in *americana* (Fig. 11B:f) and *testacea* (Fig. 10B:f), the end apparatus is located at the ends of long ductules, well separated from the exocrine pores.

Width and Sinuosity of the HSD-Sulcus.—In the primitive condition the hsd-sulcus is wider and is not straight, as in *gracilis* (Fig. 14A). In the most derived condition the sulcus is extremely narrow and very straight (Fig. 13B, 18D). The relatively wide and sinuous primitive condition is probably a result of the fact that the exocrine glands are close to the pores, such that the pores must be offset slightly one from the other. This is not necessary in the derived condition, as the exocrine glands are separated from the pores by long ductules.

The direction of change of each of these morphoclines is the same as the polarity of the morphocline of increasing numbers of elytral series of punctures (Berthélemy, 1986; Perkins, 1989). These corresponding morphoclines provide very compelling evidence of the direction of morphological change in the evolution of an ecologically effective *Hydraena*, and consequently its component phylogenetic groups.

Subgenus *Haenydra* Rey

(Fig. 10A; 13A; 14A; 17C, D; 21A)

This taxon has been treated as both a genus and a subgenus, recently by the same author. The differences between the published opinions of Jäch (1988, 1992b) obviously result from the phylogenetic evidence and reasoning presented in the interim by Perkins (1989) and Hansen (1991). Nevertheless, Jäch (1992b: 79) does not cite these works in his vacillating argument, which terminates in the statement, "The question whether *Haenydra* should be treated as a subgenus or genus is merely a technical one."

Subgeneric status for *Haenydra* is well corroborated by the hypomerai structure. Having the plesiomorphic condition for all of the characters studied, it is now clear that among known, extant *Hydraena*, the *Haenydra* line is the earliest (or among the earliest) to diverge.

One might consider elevating *Haenydra* to full generic status, were it not for the fact that *Haenydra* possesses the initial stages of those features that probably contributed greatly to the "bloom" of the lineage: the ESDS, the antennal cleaner, and the postocular sensilla. Additionally, there is no strong synapomorphy for the species of "*Hydraena*" that would remain.

For these reasons, plus the other strong synapotypic characters known for *Hydraena* (sensu lato; Perkins, 1989), plus the fact that intermediate elytral configurations exist between *Haenydra* and *Hydraena* (sensu stricto), plus the monophyly inferred from the aedeagal shape and lack of parameres (Orchymont, 1930), *Haenydra* is retained as a subgenus.

Subgenus *Hadrenya* Rey

This taxon has a checkered history. Described as a subgenus of *Hydraena* by Rey (1886), it was synonymized with the subgenus *Haenydra* by Orchymont (1925), reinstated to a valid subgenus by Berthélemy (1986), included in *Hydraena* (sensu stricto) by Jäch (1988), treated as a valid subgenus by Hansen (1991), and again included in *Hydraena* (sensu stricto) by Jäch (1992b).

This taxonomic instability stems from misapplication of the fact that the type species of this taxon, *minutissima* Stephens (= *atricapillus* Waterhouse), and other species usually placed in *Hadrenya*, have the primitive elytral stria configuration, but lack any identifiable synapomorphies.

Following Jäch (1988, 1992b) and placing these species in *Hydraena* (sensu stricto) is not merely a technical mistake, it makes that taxon a polyphyletic one. This is because another currently recognized taxon, the subgenus *Phothydraena*, is phylogenetically more closely related to the remaining, more derived species of *Hydraena* (sensu stricto), than are any of the species placed in the subgenus *Hadrenya*.

Some hypomeral features of *H. minutissima*, *H. sharpi*, and *H. pygmaea* correlate with the basal-type elytral configuration. For example, similar to the condition found in the subgenus *Haenydra*, the end-apparatus of the exocrine glands emptying into the hsd-sulcus lie just below the pores (i.e., they have very short ductules), and the pores form a slightly irregular line. However, the opening of the antennal pocket and the distribution of the hap-setae is similar to the basal state of the various configurations present in *Hydraena* (sensu stricto; i.e., derived relative to *Haenydra*).

This combination of hypomeral and elytral characters supports a hypothesis of divergence from the lineage leading to *Hydraena* (sensu stricto) occurring early, after the divergence of the subgenus *Haenydra*, and before the divergence of the subgenus *Phothydraena* (see below).

For these reasons, *Hadrenya* is hereby reinstated as a valid subgenus. It should comprise species that have a stria configuration less than (3-)a(3-)b(3-)c (a-c being nervures, see Berthélemy, 1986, and Perkins, 1989), and lacking the divergent aedeagus (no parameres) and less derived antennal pocket/hap-setae configurations of *Haenydra*.

In addition to *minutissima* (the type species), *sharpi* and *pygmaea* are included in this subgenus. Placement of other species in *Hadrenya*, or transferral from *Hadrenya* to *Hydraena* (sensu stricto) should be based on study of transparency mounts and SEM.

Most systematists agree that generic level taxa should correspond to the criteria of monophyletic sister groups. If strong synapomorphies (especially ones ecologists can see!) are demonstrated, then generic-level taxa, instead of subgenera, should be used.

Subgenera, in my view, must necessarily meet a sufficient subset of these strict phylogenetic criteria. A subgenus should never (knowingly) be polyphyletic. Nor should a subgenus be paraphyletic in the sense of having relatively underived species lumped together (because of symplesiomorphy) with species that form a monophyletic group. However, having satisfied these criteria, a subgenus for species arising near the base of a lineage serves to highlight the need for additional study.

Subgenus *Phothydraena* Kuwert
(Fig. 10B; 16A, B; 18; 20A, B)

This taxon, represented by the type species *H. testacea*, has several features of the hypomeron that suggest a divergence after *Haenydra* and *Hadrenya*, and near the base of *Hydraena* (sensu stricto). This evidence is consistent with the "intermediate" stria configuration of *Phothydraena*.

The common ancestor of the *Hydraena* lineage, after the divergence of *Haenydra*, probably had the antennal pocket and hap-setae similar to that present in *H. riparia*. From this grade can be derived the two different forms: *Phothydraena* and the more derived forms of *Hydraena* (sensu stricto).

In *Hydraena* (sensu stricto), and more so in *Haenydra*, the secretion-spreading surface exists on each side of the hsd-sulcus. In other words, between the hsd-sulcus and the lateral extreme of the hydrofuge pubescence, the cuticle is smooth. Contrastingly, in *testacea* the hydrofuge is virtually contiguous with the hsd-sulcus, and the hypomeral carina is narrow and quite convex. This structural arrangement appears to be synapomorphic for *Phothydraena*.

The hap-setae of *testacea*, although arrayed adjacent to the antennal pocket, are not positioned on the anterior extreme of the hypomeral carina, as they are in *Hydraena* (sensu stricto). Their position appears more derivable from the configuration found in *riparia*, than from the condition where the hap-setae are present on the anterior extreme of the hypomeral carina, as in most *Hydraena* (sensu stricto).

These structures, plus the less derived (not tightly clustered) antennal cleaner, seem to support the current placement of *Phothydraena* based on the intermediate elytral stria configuration, and the synapomorphies discussed by Berthélemy (1986). Consequently, subgeneric status for *Phothydraena* is supported.

Subgenus *Hydraenopsis* Janssens, **new synonymy**

This taxon is based solely on the reduced condition of the parameres. Previously, I illustrated that paramere size and placement are highly variable, and synonymized *Hydraenopsis* with *Hydraena* (Perkins, 1981:62). Berthélemy (1986: 183) concurred with this placement, based on the fact that the type species of *Hydraenopsis* has 15 elytral striae, a derived condition, synapomorphic for *Hydraena* (sensu stricto). Nevertheless, Jäch (1986:22) raised *Hydraenopsis* to a distinct subgenus of *Hydraena*: "I believe that [*Hydraenopsis* forms] a monophyletic group which is quite difficult to define because most of the character states are plesiomorphic."

Clearly, the hypomeron of "*Hydraenopsis*" has the derived condition(s) described above. These derived states are shared with many temperate species of *Hydraena* (sensu stricto) that possess the plesiomorphic condition for the aedeagus: parameres inserting basally (e.g., *circulata* group). Are we to consider this group *Hydraenopsis*? This would make the two largest subgenera ill-defined and result in abundant uncertain and unsupportable species' placement, where distribution (European vs. non-European?) "defines" taxa. In contrast, the subgenus *Hydraena* (sensu stricto) that is based on the derived elytral stria configuration is both accurate and practical.

The fact that all of the elytral stria configurations of *Hydraena* are represented in the Palearctic fauna, and that species with intermediate stria configurations are found *only* in the Palearctic surely indicates that the maximum stria configuration

of *Hydraena* (sensu stricto) evolved in Laurasia, and that tropical clades with this same configuration did not evolve that configuration in Gondwanaland. The hypomeral morphoclines correspond completely with those of the elytral stria duplications. *Hydraenopsis* is therefore reduced (again) to synonymy with *Hydraena*.

Subgenus *Spanglerina* Perkins, **new synonymy**

In an earlier paper (Perkins, 1989:455) I reduced *Spanglerina* Perkins, 1981, to a subgenus, and suggested that this status be used until the structures of *Hydraena* are more completely known. Study of transparency mounts reveals that the hypomeral structure of *Spanglerina* is similar to that of *Hydraena* (sensu stricto). *Spanglerina* is therefore hereby synonymized with *Hydraena*.

The hap-setae configuration in this group (properly termed the *ingens* species group), differs slightly from the usual for *Hydraena* (sensu stricto), as perhaps one might (now) expect, given the unusual microhabitat of species in this group: leaf packs trapped behind boulders in Neotropical streams (Perkins, 1981).

Genus *Adelphydraena* Perkins (Fig. 52, 53)

The primitive features of the mouthparts, antennae, and elytra of the genus *Adelphydraena*, as well as the features synapomorphic with *Hydraena*, were described by Perkins (1989). The postocular, genal, and hypomeral features described below differ markedly from those of *Hydraena*, corroborating the separate generic status.

The postocular and genal areas (on each side of the antennal groove; Fig. 52A, B) are clothed in hydrofuge pubescence, but lack all of the derived cuticular features described above for *Hydraena* (i.e., peg sensilla, grooved sensilla, and genal antennal pocket setae). Derived genal features unique to *Adelphydraena* include a bottle-shaped sensillum (Fig. 53B:l) located in a shallow depression medial to the antennal groove, and three very long flagelliform setae (Fig. 53B:g) located on the medial margin of the shallow depression.

Unlike *Hydraena* the antennal pocket does not open ventrally, the ventral margin being closed by the hypomeron, which bears two setae (Fig. 52:b). An antennal cleaner is not present, the medial margin of the antennal pocket having only a few simple setae (Fig. 53:f).

The hydrofuge pubescent part of the hypomeron is shaped differently than that of *Hydraena*, being lobe-shaped in the anterior part (Fig. 52C, D). In this lobe-shaped part are many hemispherical "globules"—presumed exocrine secretions (Fig. 52D:s). Also present in this area are relatively large setae that appear to be basiconic (Fig. 52D:h). When treated with strong potassium hydroxide, the hydrofuge setae remain, but the presumed basiconic sensilla are removed (Fig. 53C:r).

Although a distinct hypomeral carina is present, no hypomeral exocrine secretion groove was found. However, additional study is needed to determine the distributions of exocrine glands associated with the hypomeron.

Unique to this genus is a chemosensory/secretory fovea located laterally on the fifth abdominal sternum (Fig. 53E:x). The fovea, present in both sexes, has basiconic sensilla (Fig. 53F:t) and what appear to be secretion globules. In common with *Hydraena*, the last sternum of females has a pair of sensory clusters (Fig. 53E:y).

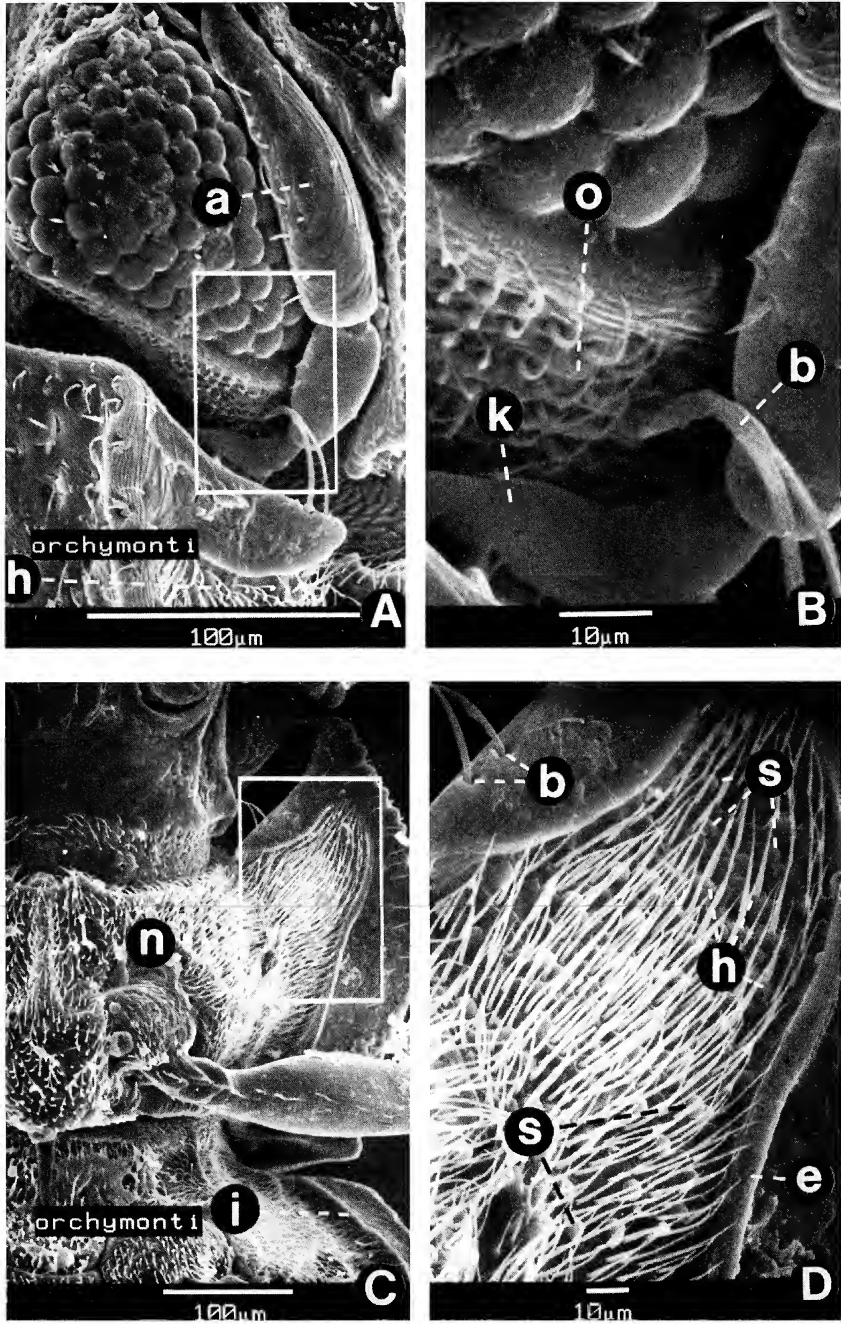


Fig. 52.—*Adephadraena orchymonti*. A. Eye and prothorax, lateral aspect of right side. B. Rectangular area of A, enlarged. C. Prothorax, ventral aspect of left side. D. Rectangular area of C, enlarged. Structures: (a) first antennomere, (b) marginal setae of antennal pocket, (e) hypomerical carina, (h) hydrofuge setae and basiconic sensilla, (i) carina of elytral epipleuron, (k) cupule article of antenna, (n) prosternum, (o) postocular hydrofuge, (s) presumed exocrine secretion.

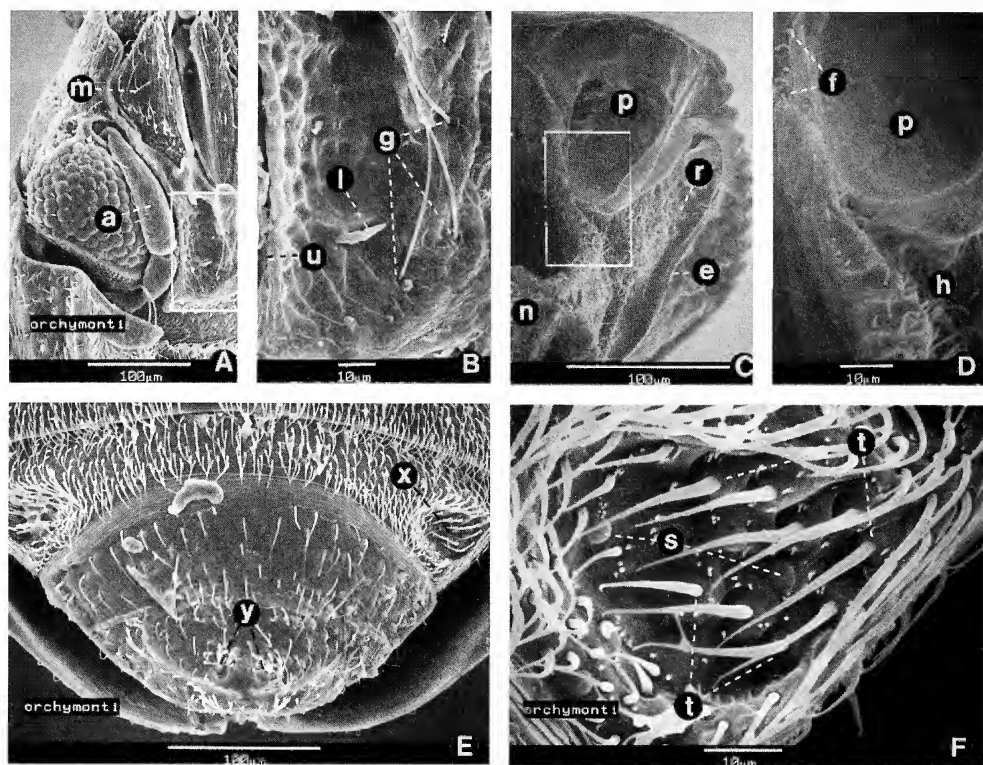


Fig. 53.—*Adephydraena orchymonti*. A. Head and anterior part of prothorax, lateral aspect of right side. B. Rectangular area of A, enlarged. C. Prothorax (treated with hydroxide), ventral aspect of left side. D. Rectangular area of C, enlarged. E. Abdominal apex, ventral aspect. F. Sensory fovea of abdomen. Structures: (a) first antennomere, (e) hypomerical carina, (f) setae on medial margin of antennal pocket, (g) genal setae, (h) hydrofuge of hypomeron, (l) bottle-shaped sensillum, (m) mandible, (n) prosternum, (p) antennal pocket, (r) sockets of hypomerical basiconic sensilla, (s) presumed exocrine secretion, (t) sensory setae, (u) subocular antennal groove, (x) sensory fovea of abdomen, (y) sensory clusters of last abdominal sternum.

Tribe Hydraenidini Perkins

This tribe comprises the three South American genera *Hydraenida*, *Parhydraenida*, and *Haptaenida*. Although many of the characters that diagnose members of this tribe are probably plesiomorphic, the species have a general external similarity, and have the two presumed synapomorphic characters given below.

Members have the following hypomerical features (numbers 3 and 4 probably apomorphic): (1) the antennal pocket is located in the anterior face of the hypomeron, at least partially closed ventrally by the anterior extreme of the hypomeron; (2) the setae on the anteroventral margin of the antennal pocket are very small, not pocket-forming; (3) the nonmarginal setae on the anterior part of the wet-hypomeron are long and flexible; and (4) the hypomerical carina is contiguous (or nearly so) with the notosternal suture, hence the hydrofuge pubescence is restricted to the postcoxal pronotal projection (Fig. 54A, B).

Retained plesiomorphic features of the Hydraenidini include the following: (1) the antenna has 11 articles (six + club), (2) the postocular area lacks specialized

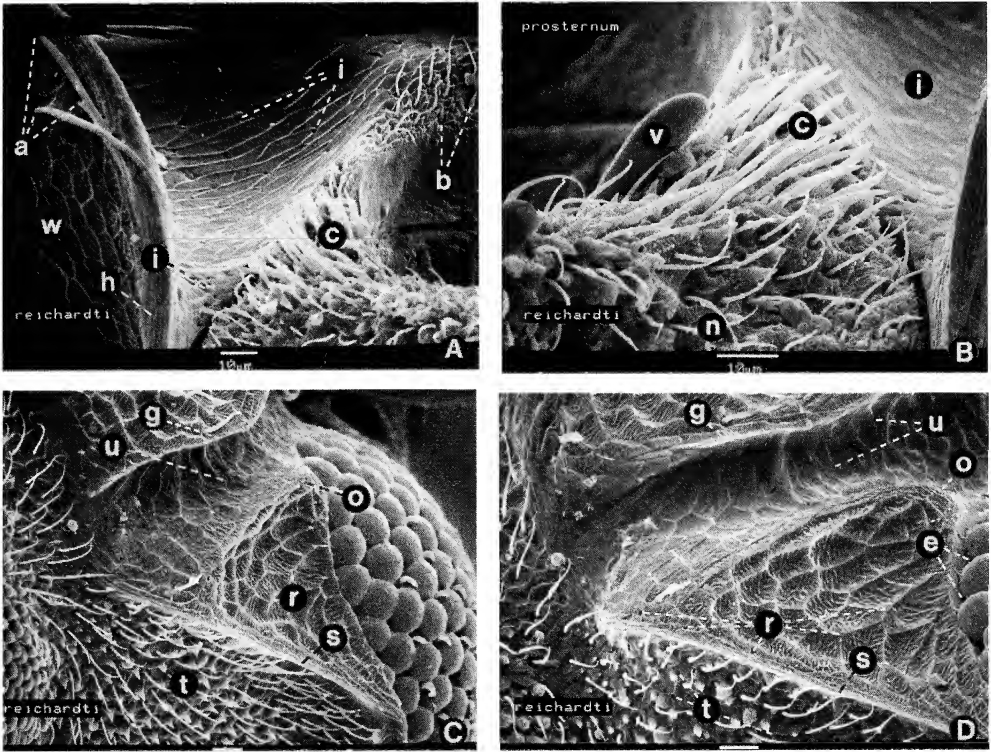


Fig. 54.—*Parhydraenida reichardti*. A. Antennal pocket area of prothorax, right side. B. Prosternum. C. Eye and subocular area, posteroventral aspect. D. Subocular area, ventrolateral aspect. Structures: (a) hypomerale flexible setae, (b) bottle-shaped sensilla, (c) antennal cleaner of prosternum, (e) pericocular pores, (g) genal ridge of subocular antennal groove, (h) hypomerale carina, (i) antennal pocket and exocrine pores, (n) prosternum, (o) exocrine pore cluster, (r) postocular triangular reticulate area and exocrine pores, (s) postocular ridge, (t) postocular asperite hydrofuge and exocrine pores, (u) subocular antennal groove and exocrine pores, (v) cervical sclerite, (w) wet-hypomerone.

sensilla, and (3) the pronotum has single (nonpaired) punctation. The last sternum, in both sexes, is largely exposed and bears setae.

Genus *Parhydraenida* Balfour-Browne

(Fig. 54)

Discussion.—The genus *Parhydraenida*, currently comprising nine species from southeastern Brazil and Ecuador, is comparatively uniform in external morphology among the species. The following description is based on SEM preparations of *P. reichardti* and transparency mounts of *P. bubrunipes*.

Description.—**Antennal pocket.** Pericocular exocrine pores (Fig. 54:e) are present at the posterior margin of the eye. The subocular antennal groove (Fig. 54:u) is deep, its medial margin cariniform, forming a distinct channel. A postocular triangular reticulate area (Fig. 54:r) is located at the posteroventral angle of the eye. This triangular area lacks hydrofuge pubescence and has exocrine pores at the intersects of some of the microreticulations (Fig. 54:r), and a small cluster of pores (e.g., ca. ten in *P. bubrunipes*) at the anterior angle of the triangular area (Fig. 54:o). A sharp postocular carina (Fig. 54:s) forms the posterior rim of the triangular reticulate area, and separates the latter from the postocular asperite hydrofuge (Fig. 54:t). The postocular area lacks any specialized exocrine secretion delivery setae or sensilla.

A well-developed, rounded hypomeral carina (Fig. 54:h) separates the wet- and much smaller bubble-hypomeron. Anteriorly, the hypomeral carina is contiguous (or nearly so) with the notosternal suture, hence the hydrofuge pubescence of the bubble-hypomeron is entirely (or nearly so) restricted to the notal postcoxal projection.

The wet-hypomeron (Fig. 54:w) is wide, microreticulate, and has random exocrine pores at some of the intersects of the microreticulation. In one species, *P. bubrunipes*, these pores are extremely dense over the lateral three-fourths of the wet-hypomeron, but absent over the medial fourth (including near the carina). There are neither organized clusters of pores, nor a secretion sulcus on the hypomeron.

Near the anterior extreme of the wet-hypomeron, set back from the margin, are six to eight elongate hypomeral flexible setae (Fig. 54:a). These setae are flexible in their sockets, and are not rigid enough, nor appropriately placed, to form part of the antennal pocket. Present on the anterior margin of the antennal pocket, but not large enough to form part of the antennal pocket, are a few very small setae, about five in number.

The antennal pocket (Fig. 54:i) is deep, lacking hydrofuge pubescence, the surface microreticulate and having randomly distributed, moderately dense exocrine pores. The pores are more concentrated at the posterior extreme of the antennal pocket. Medial to the antennal pocket, the notal area is asperite hydrofuge and has two bottle-shaped sensilla (Fig. 54:b).

A dense cluster of sharp spines and stiff setae, the prosternal antennal cleaner (Fig. 54:c) is located at the anterolateral angle of the prosternum. Some of the setae in this spine cluster appear to be shallowly grooved; it is possible that some are chemoreceptors. The antennal cleaner is surrounded by asperite hydrofuge.

Genus *Hydraenida* Germain

Discussion.—The genus *Hydraenida* currently comprises two species from Chile, *H. ocellata* and *H. robusta*. The following description is based on transparency mounts of both of these species.

Description.—**Antennal pocket.** The distinctive reticulate, triangular postocular area of *Parhydraenida* is absent in *Hydraenida*, the corresponding area with smooth cuticle and lacking a ridge. However, exocrine pores are found in corresponding locations in the two genera: in *Hydraenida* a tight cluster of about 12 pores is present in the location corresponding to the ridge-mounted exocrine pore cluster of *Parhydraenida* (Fig. 54C:o), and a separate group of pores, about 12, is present in the area corresponding to the reticulate triangular area of *Parhydraenida* (Fig. 54C:r). The postocular carina is present in both genera (Fig. 54C:s).

The hypomeron differs from that of *Parhydraenida* as follows: (1) a narrow, smooth, and nonhydrofuge pubescent gap exists between the hypomeral carina and the notosternal suture (these structures being contiguous in *Parhydraenida*); (2) the margin of the hypomeron at the antennal pocket is less arcuate; (3) the prominent, flexible, and loosely socketed setae near the anterior margin of the hypomeron of *Parhydraenida* (Fig. 54A:a) are apparently absent (more specimens of *Hydraenida* are needed to confirm this); (4) the smooth area between the hypomeral carina and the hydrofuge of the postcoxal projection is slightly wider in *Hydraenida*; and (5) the posterior area of the hypomeron is wider in *Hydraenida*, correlated with the nonsinuate posterior sides of the prothorax. Apparently the prosternum of *Hydraenida* lacks the antennal cleaning cluster of spines present in *Parhydraenida* (Fig. 54B:c). However, more specimens and SEM study are needed to confirm this.

Haptaenida, new genus

Type Species.—*Haptaenida huggerti*, new species.

Diagnosis.—Recognized by the laterally open antennal pockets (Fig. 55), the 11 articles of the antenna (six + club), the ocelli located closer to the midline than to the eyes, the moderately short maxillary palpi with length ratios of last three articles as six:three:seven, the transverse, noncordiform pronotum with anterior and posterior hyaline margins, the posteriorly narrowed and transversely convex elytra, the restricted abdominal hydrofuge pubescence, the very large wet-hypomeron, and the features of the postocular/hypomeral antennal pocket (see morphological section).

Description.—**Antennal pocket.** The postocular area and the hypomeron of *Haptaenida huggerti*,

n. gen., n. sp. (formally described in a following section) differ from *Parhydraenida* in the following respects (no slide mounts studied). In the postocular area, the region corresponding to the distinctive reticulate triangular area of *Parhydraenida* (Fig. 54C:r) is shining and shaped differently in *Haptaenida*, being more elongate and medially arcuate. The antennal subocular sulcus is wider in *Haptaenida* than in *Parhydraenida*. The postocular carina is present in both genera (Fig. 54C:s).

The hypomeron has the ventral opening to the antennal pocket wider than in *Parhydraenida*. The prominent, flexible, and loosely socketed setae near the anterior margin of the hypomeron of *Parhydraenida* (Fig. 54A:a) are apparently absent (more specimens are needed to confirm this). In addition to these differences, the antennal pocket is open in lateral aspect in *Haptaenida* (Fig. 55), and closed in *Parhydraenida*. Apparently the prosternum of *Haptaenida* lacks the antennal cleaning spines present in *Parhydraenida* (Fig. 54B:c). However, more specimens and SEM study are needed to confirm this.

Other characters. Body size moderate, form elongate oval and posteriorly narrowed, weakly convex, elytra more strongly so, head not deflexed. Antennomeres 11 (six + club), third slightly longer than combined lengths of fourth to sixth. Maxillary palpi moderately long, length ratios of articles two to four (last) as six : three : seven. Eyes rather small, not elevated. Gena with low transverse ridge behind cardo. Labrum moderately large, not set at angle to clypeus, apicomedialely emarginate; anterior margin fringed with setae. Clypeus anterior margin straight. Ocelli small and weakly convex, each located twice as far from eye as from midline, frons not convex between ocelli; area behind and between ocelli lacking carinae. Pronotum with anterior transverse fovea broadly joined to lateral depressions; a short, shallow transverse fovea behind midlength; sides from midlength to anterior angles straight and slightly convergent, from midlength to posterior angles more strongly convergent and slightly concavely arcuate. Anterior hyaline border narrow, present in weak emargination over median half of anterior margin. Posterior hyaline border very narrow. Elytra with weak rows of punctures, becoming more irregular laterally. Antennal pocket large, shining, open ventrally and laterally. Prosternum in front of procoxae shorter than procoxal cavities, latter open behind. Metasternum reduced, shorter than mesosternum, with shallow midlongitudinal impression. Intercostal sternite small, triangular. Legs and tarsi short, tarsi apparently five-five-five (no slide mount). Both sexes with abdominal sterna one to four about equal in length, fifth slightly longer than fourth; seventh visible beyond posterior margin of sixth; first and lateral thirds of second hydrofuge pubescent, remainder with sparse, more robust setae. Hydrofuge pubescence also present on postocular area, bubble-hypomeron (except antennal pockets), notal postcoxal projections, mesosternum, and metasternum. Wingless.

Etymology.—Greek, *hapt* (join, lay hold of) plus *aenida* (from *Hydraenida*), in reference to the unusual aedeagus and flightlessness; gender feminine.

Haptaenida huggerti, new species

(Fig. 55, 56)

Type Material.—Holotype male and one paratype of each sex: Ecuador, Napo, Quito-Baeza road, 4,100 m, iii.1983, leg. Huggert and Masner; deposited in MCZ.

Description.—Size (mm × 100; length/width): body 224/89, head 42/60, pronotum 51/80, elytra 128/89. Dorsum black to dark brown, with inconspicuous setae; legs and maxillary palpi brown. Labrum and clypeus dull, micropunctulate. Frons shallowly, densely punctate, dull. Labroclypeal suture shallow. Shallow, densely micropunctulate depression between eye and ocellus. Pronotal disc moderately densely, shallowly punctate, interstices shining, 0.5–2.0 times puncture diameter, becoming more densely punctate laterally. Elytra with ten slightly irregular series of shallow punctures, each puncture with a fine, short, granule-based seta; intervals with similar granule-based setae, slightly denser on intervals four, six, and eight, interval eight slightly raised. Last abdominal sternum, in male, apically truncate; in female strongly arcuate. Last tergum, in male, apically truncate and with a patch of setae on each side; in female weakly arcuate and with shorter setae than in male. Aedeagus (Fig. 56) lacking parameres and with two large distal processes; length 0.51 mm.

Etymology.—Named in honor of Lars Huggert, who collected the specimens.

Discussion.—Anders Nilsson kindly provided the following information on the type locality: “The specimens were collected in a small lake (ca. 10 × 10 m) on open ground. Most of the area was peaty with scattered elfin forest, but the lake was surrounded by mineral (morainic) ground. The beetles were collected at the lake margin among stones and silt. There was almost no vegetation in the lake and some low grasses on the surrounding ground. It was very windy, with eastern winds prevailing, from the Amazonas.”

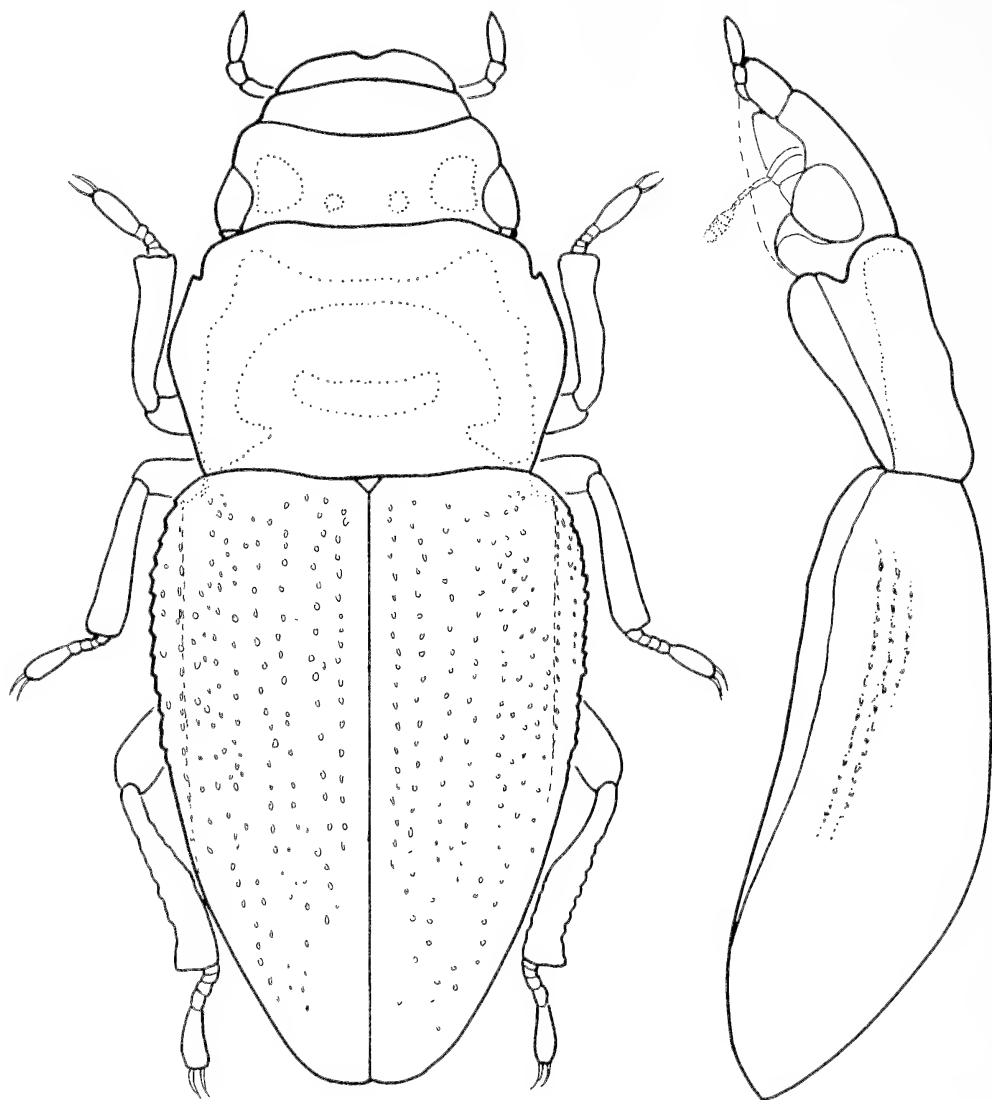


Fig. 55.—*Haptaenida huggerti*, dorsal and lateral aspects.

Parhydraenini, new tribe

This tribe comprises the genera *Pneuminion* n. gen., *Parhydraena*, *Protozantaena* n. gen., and *Discozantaena*. Members of the tribe are characterized by the following presumed synapomorphic characters: (1) the antennal pocket is formed by stiff, arcuate hypomeral setae the most medial of which emerge from the anterior extreme of the hypomeral hydrofuge (secondarily reduced in *Discozantaena*); (2) the prosternum has a cluster of specialized spines on each side ("zantes" = presumed antennal cleaner); and (3) the pronotum has distinctive "paired" punctuation.

Additional diagnostic features, presumably plesiomorphic include: (1) the post-

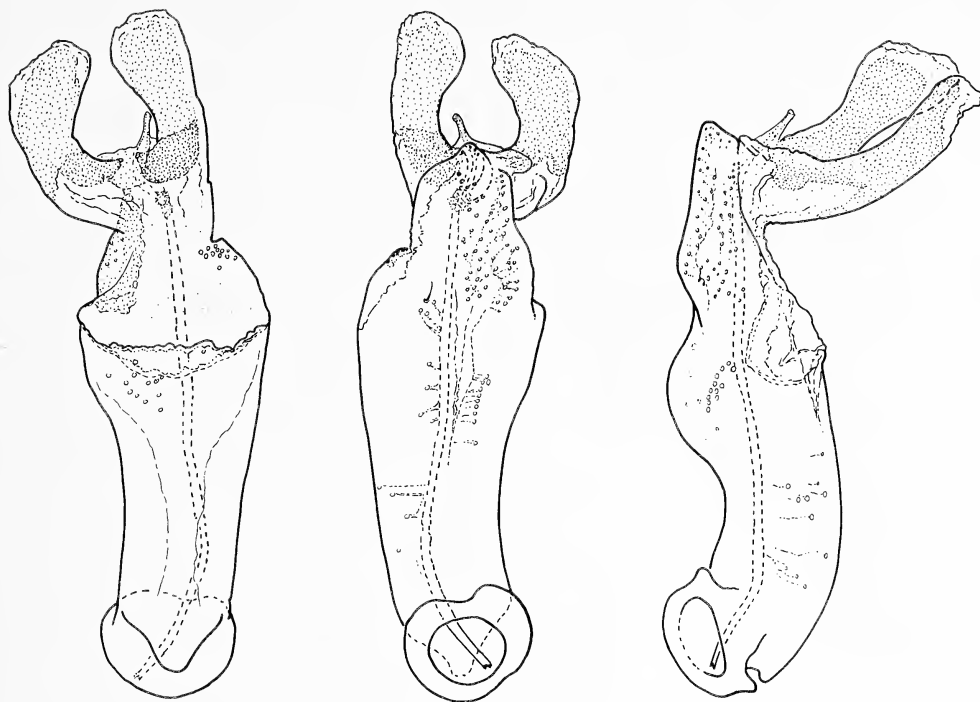


Fig. 56.—*Haptaenida huggerti*, aedeagus of holotype.

ocular area lacks specialized sensilla, (2) the hypomeral hydrofuge attains the antennal pocket, and (3) the wet-hypomeron lacks elongate and flexible setae.

The genera *Protozantaena* and *Discozantaena* share an unusual derived aedeagus having a characteristic shape, long terminal flagellum, and very short parameres. The genus *Pneuminion* can be considered to have branched off early in this clade, based on the retained ancestral condition of 11 antennomeres (the three other genera having ten antennomeres). This early divergence is also suggested by the “reversed” architecture of the antennal pocket—open dorsally via post-ocular emargination of the pronotum, and closed ventrally by the anterior part of the wet-hypomeron.

Pneuminion, new genus

Type Species.—*Pneuminion velamen*, new species.

Diagnosis.—Recognized by the 11 articles of the antenna (six + club), the ocelli located midway between the midline and the eyes, the moderately short maxillary palpi with length ratios of last three articles as five:four:eight, the transverse, noncordiform pronotum lacking hyaline margins and with well-developed postocular emarginations, the elytra with ten very regular series of very shallow punctures and all interseries equally developed, the restricted abdominal hydrofuge pubescence, the very large wet-hypomeron, and the features of the postocular/hypomeral antennal pocket (see morphological section).

Description.—**Antennal pocket**. The hypomeral carina is well defined, angulate posteriorly, and

becomes obsolete anteriorly at the antennal pocket. The bubble-hypomeron is narrow and very sparsely pubescent opposite the notosternal suture.

The wet-hypomeron is very wide, slightly wider anteriorly than posteriorly, reticulate, nonsetose (except hap-setae), and with very sparse, randomly distributed exocrine pores. A row of 12–15 well-developed hypomeral antennal pocket setae are located along the ventral margin of the antennal pocket; these setae are closely spaced, each widest in the middle, tapering apically, and flattened. The setae become progressively longer from the most lateral to the most medial, the latter arising from the anterior extreme of the hydrofuge hypomeron, adjacent to the lateral extreme of the procoxal cavity. There are no organized clusters of exocrine pores or end-apparatus, and no secretion sulcus exists on the hypomeron.

The antennal pocket is located in the anterior face of the prothorax, moderately deep, opened ventromedially (between the hap-setae and the prosternum) and dorsally (at the postocular emarginations); the middle portion of the pocket is convex, partially dividing the pocket into a dorsal and a ventral concavity. About nine exocrine pores are located along the medial margin of the pocket, next to the notosternal suture; otherwise the pocket has very few, randomly distributed exocrine pores.

A dense cluster of sharp spines, the prosternal antennal cleaner is located on the anterolateral margin of the prosternum. The antennal cleaner is surrounded by sparsely pubescent asperite hydrofuge.

Periocular exocrine pores are present along the subocular antennal groove and at the posterior margin of the eye. The medial margin of the antennal groove is raised slightly, not cariniform. A few exocrine pores are located near the posteroventral angle of the eye. A well-developed postocular ridge delimits the postocular and subocular areas. The postocular area is clothed in hydrofuge pubescence, but lacks any specialized exocrine secretion delivery setae or sensilla.

Other characters. Body size moderate to small, form elongate oval, moderately convex dorsally, head not deflexed. Antennomeres 11 (six + club), third slightly longer than combined lengths of fourth to sixth. Maxillary palpi moderately short, length ratios of articles two to four (last) as five:four:eight. Eyes well developed, not elevated. Labrum large, set at angle to clypeus, apicomediaally deeply incised; anterior margin fringed with long setae. Clypeus anterior margin straight. Ocelli located midway between midline and eyes, frons very weakly convex between ocelli; area behind and between ocelli lacking carinae. Pronotum with anterior midlongitudinal fovea, behind which is a U-shaped fovea; lateral depressions not demarked by foveae; lateral margin arcuate. Hyaline borders absent; setal fringe on base in front of scutellum. Elytra with ten rows of punctures. Antennal pocket as described in morphology section. Prosternum in front of procoxae shorter than procoxal cavities, latter open behind. Metasternum with shallow midlongitudinal impression. Intercoxal sternite small, triangular. Legs moderately elongate, tarsi five–five–five. Abdominal sterna one to four about equal in length, fifth slightly longer than fourth; in male, seventh concealed beneath sixth; in female seventh visible beyond posterior margin of sixth; first and basal part of second hydrofuge pubescent, remainder with sparse, fine, long setae. Hydrofuge pubescence also present on postocular area, bubble-hypomeron (except antennal pockets), notal postcoxal projections, mesosternum, and metasternum.

Etymology.—Greek, *pneum* (breathe) plus *inion* (nape of the neck), in reference to the pronotal postocular emarginations of the antennal pocket; gender neuter.

Pneuminion velamen, new species

Type Material.—Holotype male and 25 paratypes: South Africa, Cape Province, Cederberg, 1130 m, sifted marsh shore, 32.28S–19.14E, 7.xi.1983, Endrody-Younga (#2055); deposited in TMSA. Additional paratypes: Cape Province, Farm Ezelsfontein, shorewashing, 30.24S–18.05E, 30.x.1977, Endrody-Younga (#1407); (4 TMSA). S. W. Cape, Hawaquas rad. tower, 33.41S–19.06E, shore washing, 27.X.1978, Endrody-Younga (#1484); (5 TMSA). Cape-Swartberg, Seweweekspoort Klf, 33.24S–21.21E, river stones, 18-XI-1973, Endrody-Younga (#269); (1 TMSA). W. Cape, Hawequas, 33.34S–19.08E, from rock pools, 6.XI.1973, Endrody-Younga (#210); (3 TMSA). S. W. Cape, Limiet Berge, 33.33S–19.07E, water collection at 950 m, 7.XI.1973, Endrody-Younga (#215); (1 TMSA). Cape, Cederberg, Eikenboom, 900m, 32.27S–19.10E, river stones, 29-X-1981, Endrody-Younga (#1906); (2 TMSA). Representative duplicate specimens deposited in MCZ and CMNH.

Description.—Size (mm × 100; length/width): body (length to elytral apices) 191/84, head 36/51,

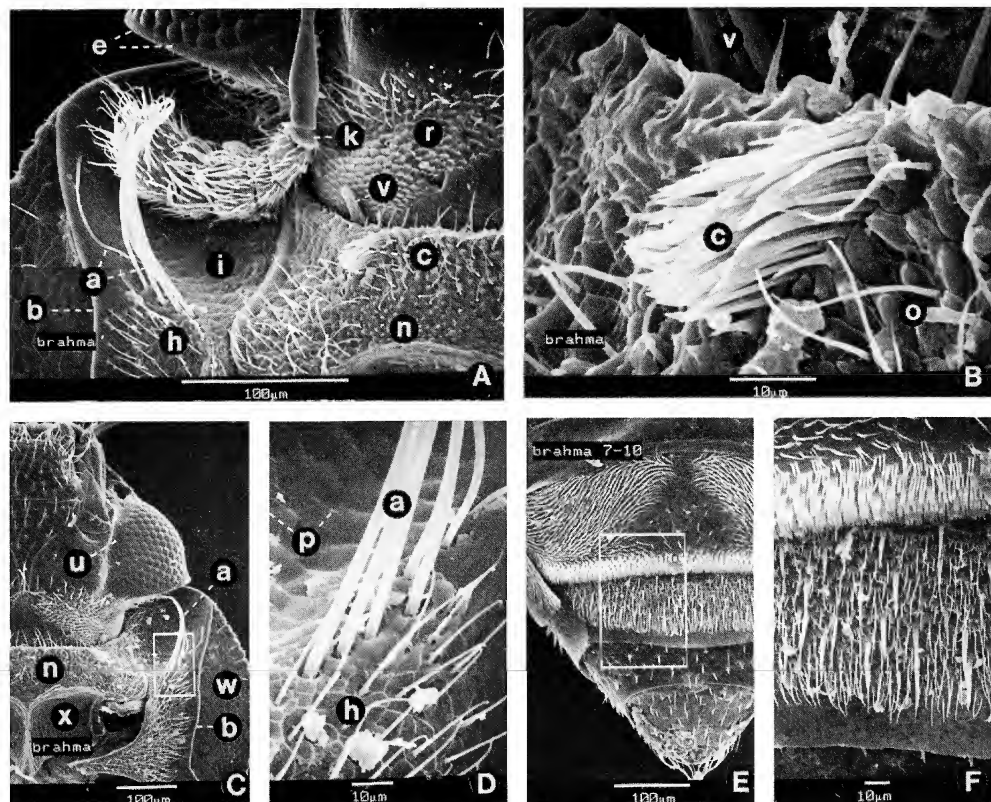


Fig. 57.—*Parhydraena* (undescribed species "BRA," from South Africa). A. Antennal pocket and associated structures, right side. B. Antennal cleaner of prosternum. C. Head and prothorax, ventral aspect of left side. D. Rectangular area of C, enlarged. E. Abdominal terga 7–10. F. Rectangular area of E, enlarged. Structures: (a) hypomerical antennal pocket setae, (b) hypomerical carina, (c) antennal cleaner of prosternum, (e) eye and periocular exocrine pores, (h) hypomerical reticulate hydrofuge, (i) antennal pocket, (k) cupule article of antenna, (n) prosternum, (o) prosternal asperite hydrofuge, (p) exocrine pores of antennal pocket, (r) genal asperite hydrofuge, (u) subocular antennal groove, (v) cervical sclerite, (w) wet-hypomeron, (x) procoxa.

pronotum 42/69, elytra 119/84. Dorsum black, with moderately dense, conspicuous white setae; legs and maxillary palpi brown. Labrum, clypeus, and frons dull, micropunctulate. Labroclypeal suture shallow. Shallow fovea in front of each ocellus. Pronotal postocular emarginations deeper and less symmetrical in females than in males. Pronotum dull, entirely micropunctulate, subrugose; oblique anterior fovea on each side shallowly connecting to midlongitudinal fovea; posterior U-shaped fovea well developed; setae at lateral margin flat on cuticle in dry specimens. Elytra with setae of series and interseries equally developed, resulting in very discrete, narrowly separated, unilinear rows of setae, about 18 on each elytron, each seta granule-based; serial punctures very shallow (but internal columellae well developed); interseries very slightly raised; explanate margin narrow in both sexes.

Etymology.—Latin, *velamen* (robe, garment), in reference to the distinctive dorsal pubescence.

Discussion.—A figure of the male genitalia of *P. velamen*, and descriptions of additional new species in the genus will be given in a separate paper.

Genus *Parhydraena* Orchymont (Fig. 57)

Discussion.—The characters described below are quite similar in all of the species of *Parhydraena* studied (see Appendix 1), including the type species *P.*

brevipalpis. The number of hap-setae varies from seven to 14. Their location relative to the hypomeral carina varies slightly, correlating with the width of the hypomeron, but their position relative to the prosternal antennal cleaner and head is more constant.

Parhydraena cooperi Orchymont, the type species of the subgenus *Pseudhydraena* Orchymont, has characteristics like those described below (12 hap-setae). The aedeagus of *P. (Pseudhydraena) cooperi* lacks parameres, and this seems to be the only distinction indicating, perhaps, a valid subgeneric status for *Pseudhydraena*.

Description.—**Antennal pocket.** A sharp, step-like hypomeral carina (Fig. 57:b) separates the wet- and bubble-hypomeron. Between the carina and the reticulate hydrofuge the cuticle is completely smooth, and has about 15 randomly spaced exocrine pores distributed along its length. There are no organized clusters of pores or end-apparatus, and no secretion sulcus exists on the hypomeron.

A cluster of well-developed antennal pocket setae (Fig. 57:a) are located at the posterior margin of the antennal pocket. These setae arise from the anterior extreme of the hydrofuge hypomeron, not from the anterior extreme of the wet-hypomeron as in *Hydraena*.

The antennal pocket (Fig. 57:i) is relatively wide and only moderately deep, lacking hydrofuge pubescence, the surface grading from smooth laterally to microreticulate medially. Within the pocket are randomly distributed exocrine pores (Fig. 57:p).

A dense cluster of sharp spines, the prosternal antennal cleaner (Fig. 57:c) is located near the anterior margin of the prosternum. This spine cluster is interpreted as an antennal cleaner based on its location and the orientation of the spines. The antennal cleaner is surrounded by asperite hydrofuge (Fig. 57:o), except the area between the cleaner and the antennal pocket, which is sharply asperite but lacks hydrofuge hairs—hence the movement of the antenna against the cleaner (when the antenna is raised during air capture) would not be impeded by hydrofuge hairs.

Periocular exocrine pores (Fig. 57:e) are present at the posterior margin of the eye and along the subocular antennal groove (Fig. 57:u). The postocular area is clothed in hydrofuge pubescence, but lacks any specialized exocrine secretion delivery setae or sensilla.

Genus *Decarthrocerus* Orchymont, **new synonymy**

Decarthrocerus jeanneli Orchymont, the type species of the genus, is similar in characteristics to those described above for *Parhydraena*. It differs in having six or seven hap-setae, only one or two fewer than the minimal number for known *Parhydraena*. This species also has a more deflexed labrum, but this is not of generic significance.

However, like *Parhydraena (Pseudhydraena)*, the aedeagus of *D. jeanneli* lacks parameres. Therefore, *Decarthrocerus* is hereby synonymized with *Pseudhydraena* Orchymont (also described in 1948, but before *Decarthrocerus*; see Hansen, 1991, for literature citations).

Protozantaena, **new genus**

Type Species.—*Protozantaena labrata*, new species.

Diagnosis.—Recognized by the small size; the ten-articled antenna (five + club); the lack of an hypomeral carina; the weakly developed ocelli located midway between the midline and the eyes; the large maxillary palpi, as long as the antennae; apical article wide; inner surface arcuate at base; length ratios of last three articles as six:four:nine; the transverse, slightly cordiform pronotum with anterior hyaline margin and lacking postocular emarginations; the female abdominal apex; the male genitalia; and the features of the postocular/hypomeral antennal pocket (see morphological section).

Description.—**Antennal pocket.** The hydrofuge hypomeron is narrow adjacent to the procoxal cavity; lateral to the hydrofuge the hypomeron is smooth, slightly convex (noncariniform), and has

sparse, random exocrine pores, about 16–20 along its length. The remainder of the wet-hypomeron is very weakly microreticulate. There are no organized clusters of pores or end-apparatus, and no secretion sulcus exists on the hypomeron. A row of 12–15 well-developed antennal pocket setae are located along the ventral margin of the antennal pocket. These setae are closely spaced, each widest in the middle, tapering apically, and flattened. The setae are progressively longer medially, the most medial arising from the anterior extreme of the hydrofuge hypomeron, adjacent to the lateral extreme of the procoxal cavity.

The antennal pocket is relatively wide and only moderately deep, not closed ventrally (except by pocket setae), lacks hydrofuge pubescence except at anteromedial extreme; a narrow band of minute spicules (in rows) is present along the medial margin. Within the pocket are randomly distributed exocrine pores.

A dense cluster of sharp spines, the prosternal antennal cleaner is located on the anterolateral margin of the prosternum. The antennal cleaner is surrounded by sparsely pubescent asperite hydrofuge.

Periocular exocrine pores are present along the subocular antennal groove and at the posterior margin of the eye. A few exocrine pores are located near the posteroventral angle of the eye. A well-developed postocular ridge delimits the postocular and subocular areas. The postocular area is clothed in hydrofuge pubescence, but lacks any specialized exocrine secretion delivery setae or sensilla.

Other characters. Body size small, form elongate oval, moderately transversely convex dorsally, head not deflexed. Antennomeres ten (five + club), second slightly longer than combined lengths of third to fifth. Maxillary palpus relatively large, as long as antenna, length ratios of articles two to four (last) as six:four:nine, apical article relative wide, inner surface arcuate basally. Eyes well developed, not elevated. Labrum large, rectangular, set at angle to and longer than clypeus, anterior margin nearly straight, fringed with long setae. Clypeus anterior margin and frontoclypeal suture very slightly arcuate. Ocelli weakly convex, located midway between midline and eyes, frons very weakly convex between ocelli; area behind and between ocelli lacking carinae. Pronotum with very indistinct, widely U-shaped fovea behind middle on disc; no foveae demarking lateral depressions; lateral margins sinuate behind midlength; anterior hyaline border present over median third, extremely narrow. Elytra with ten rows of punctures. Antennal pocket as described in morphology section. Prosternum in front of procoxae shorter than procoxal cavities, latter open behind; zantes present. Hypomeron lacking carina at margin of hydrofuge pubescence. Metasternum with shallow impression on disc in basal half. Intercoxal sternite small, triangular. Legs moderately elongate, tarsi five–five–five. Hydrofuge pubescence present on postocular area, bubble-hypomeron (except antennal pockets), notal postcoxal projections, mesosternum, metasternum, first four abdominal sterna, and basal part of fifth.

Etymology.—Greek, *proto* (first) plus *zantaena* (from *Discozantaena*); gender feminine.

Protozantaena labrata, new species (Fig. 58C)

Type Material.—Holotype male: Namibia: Naukluft, Naukluft Park, 24.16S–16.15E, shore washing, 26.x.1974, Endrody-Younga (#431); deposited in the TMSA. Paratypes: same data as holotype, (95 TMSA); same locality, water collection, (#430), (1 TMSA); same locality, river stones, 23.viii.1982, (#1921), (3 TMSA); same locality, shore washing, river, 10.viii.1989, Endrody-Younga and Klim. (#2644), (432 TMSA); same locality, flowering bushes, 11.viii.1989, (#2646), (1 TMSA); same locality, Naukluft cascades, 12.viii.1989, Endrody-Younga and Klim. (#2648), (4 TMSA). Representative duplicate paratypes deposited in CMNH, FMNH, and MCZ.

Description.—Size (mm × 100; length/width): body 140/60, head 24/42, pronotum 33/54, elytra 90/60. Color brown to dark brown, head and disc of pronotum darker than remainder, setae fine, short; legs and maxillary palpi brown to testaceous. Labrum, in male, with apical margin narrowly upturned, in female simple. Labrum, clypeus, and frons moderately shining, irregularly punctulate. Labroclypeal suture shallow. Shallow oblique fovea in front of each ocellus. Pronotal anterior margin weakly arcuate. Pronotum dull and rather densely paired-punctulate, some forming transverse rows, except smooth and shining, vaguely heart-shaped area on disc. Elytra with serial punctures small, interseries about twice width of punctures; explanate margin narrow in both sexes. Aedeagus (Fig. 58C) with greatly reduced parameres and two elongate distal flagella; length 0.46 mm (from base to bend in flagellum).

Etymology.—Latin, *labrata*, in reference to the distinctive labrum.

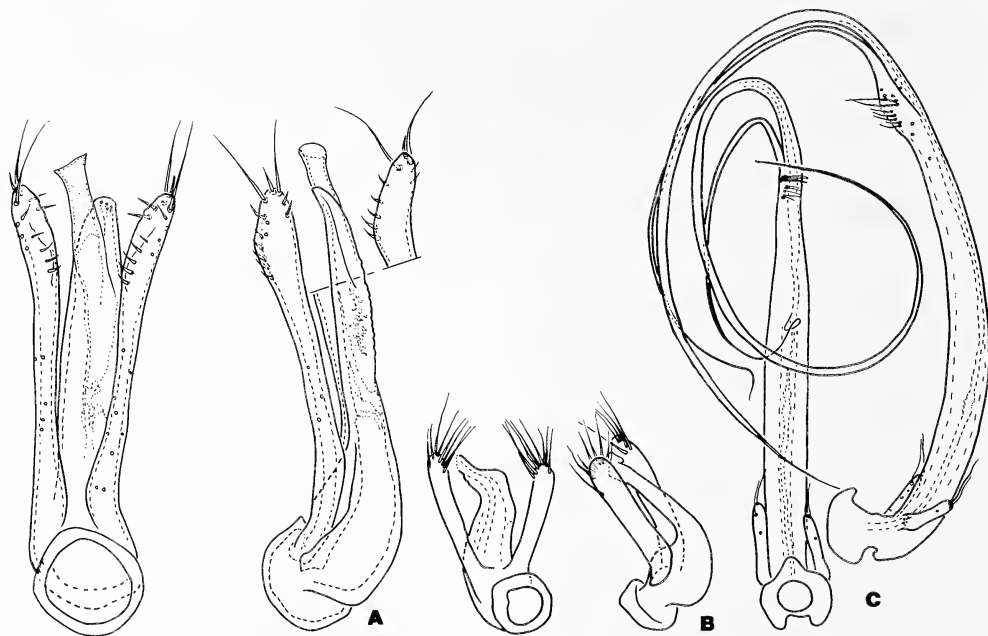


Fig. 58.—Aedeagi of holotypes. A. *Ochtheosus fungicolus*. B. *Davidraena bacata*. C. *Protozantaena labrata*.

Genus *Discozantaena* Perkins and Balfour-Browne (Fig. 59, 60)

Discussion.—The following description is based on SEM and transparency preparations of *D. genuvela* and an undescribed species from South Africa.

Description.—**Antennal pocket.** A low, rounded hypomeran carina separates the wet- and bubble-hypomeran. The carina becomes obsolete posteriorly. Exocrine pores, about 25–35 in number, are randomly distributed along the inner margin of the carina and between the carina and the reticulate hydrofuge. There are no organized clusters of pores or end-apparatus, and no secretion sulcus exists on the hypomeran.

The antennal pocket setae (Fig. 59:a) are very small, about four in number, nonrigid (lie flat on the cuticle in dry specimens) and located at the posterolateral margin of the antennal pocket. The antennal pocket (Fig. 59:i, 60:i) is relatively wide and shallow, entirely microreticulate, and has a narrow band of hydrofuge pubescence along the lateral, anterior, and anteromedial margins. Within the pocket are randomly distributed exocrine pores.

A prosternal antennal cleaner (Fig. 59:c, 60:c) is located similarly to that of *Parhydraena*, near the anterior margin of the prosternum (but differs slightly in shape and orientation). As in *Parhydraena*, there are no hydrofuge hairs between the antennal cleaner and the antennal pocket, otherwise the antennal cleaner is surrounded by reticulate hydrofuge. Exocrine pores (Fig. 59:p, 60:p) are located near the base of the antennal cleaner.

Periocular exocrine pores (Fig. 60:o) are present at the margin of the eye. The subocular antennal groove is microreticulate and has numerous exocrine pores (Fig. 59:u, 60:u). The postocular area is clothed in hydrofuge pubescence (Fig. 59:t), but lacks any specialized exocrine secretion delivery setae or sensilla.

Madagastriini, new tribe

This tribe comprises the genera *Madagaster* n. gen. (type genus), *Davidraena*, *Gondraena*, and *Coelometopon*. Like the Hydraenidini, this tribe retains several

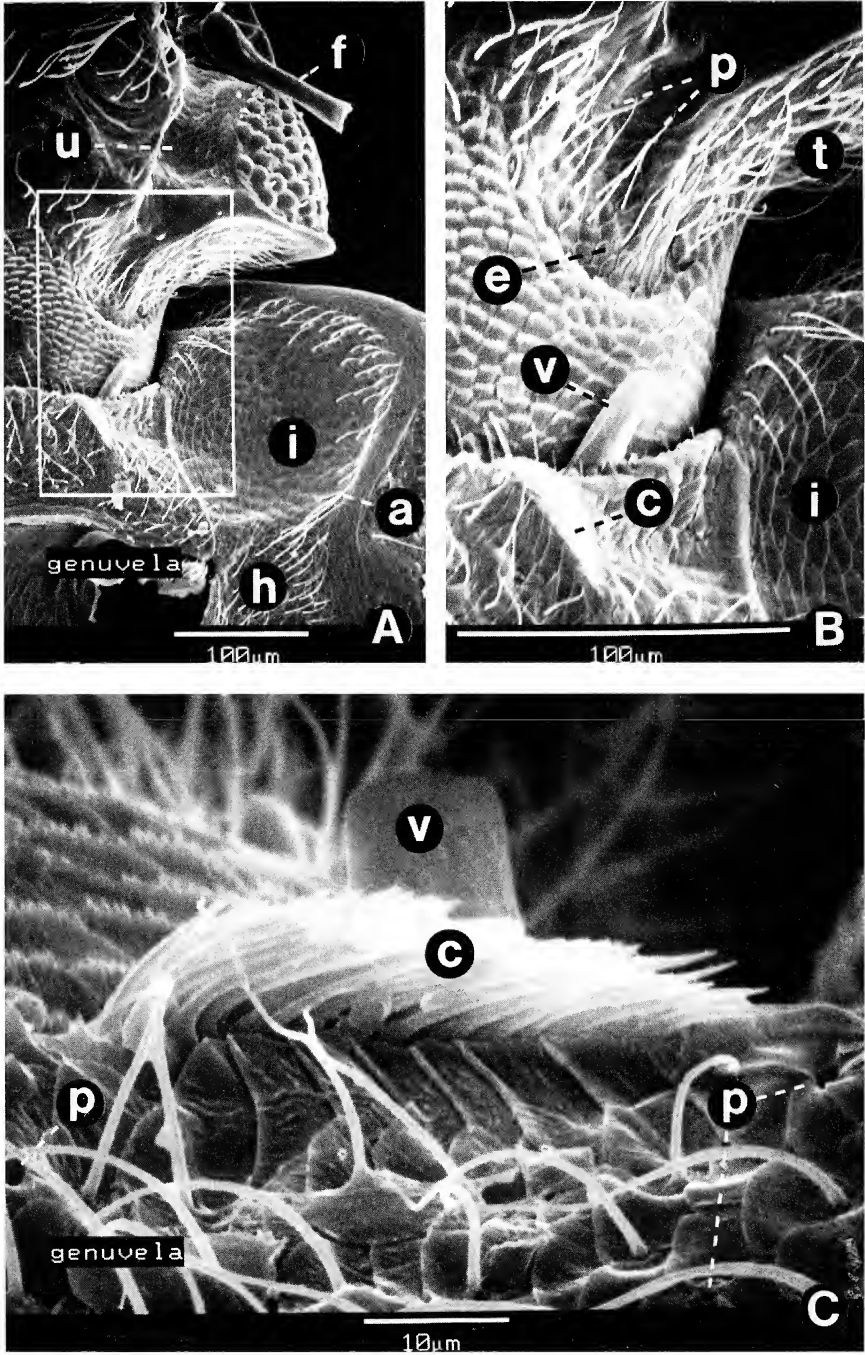


Fig. 59.—*Discozantaena genuvela*. A. Head and prothorax, ventral aspect of left side. B. Rectangular area of A, enlarged. C. Antennifer of prosthema, posteroventral aspect. Structures: (a) hypomerical antennal pocket setae, (c) antennifer of prosthema, (f) first article of antenna (remainder removed), (e) genal antennal groove, (h) hypomerical reticulate hydrofuge, (i) antennal pocket, (p) exocrine pores of (in B) subocular groove and (in C) prosthema, (t) postocular hydrofuge, (u) subocular antennal groove.

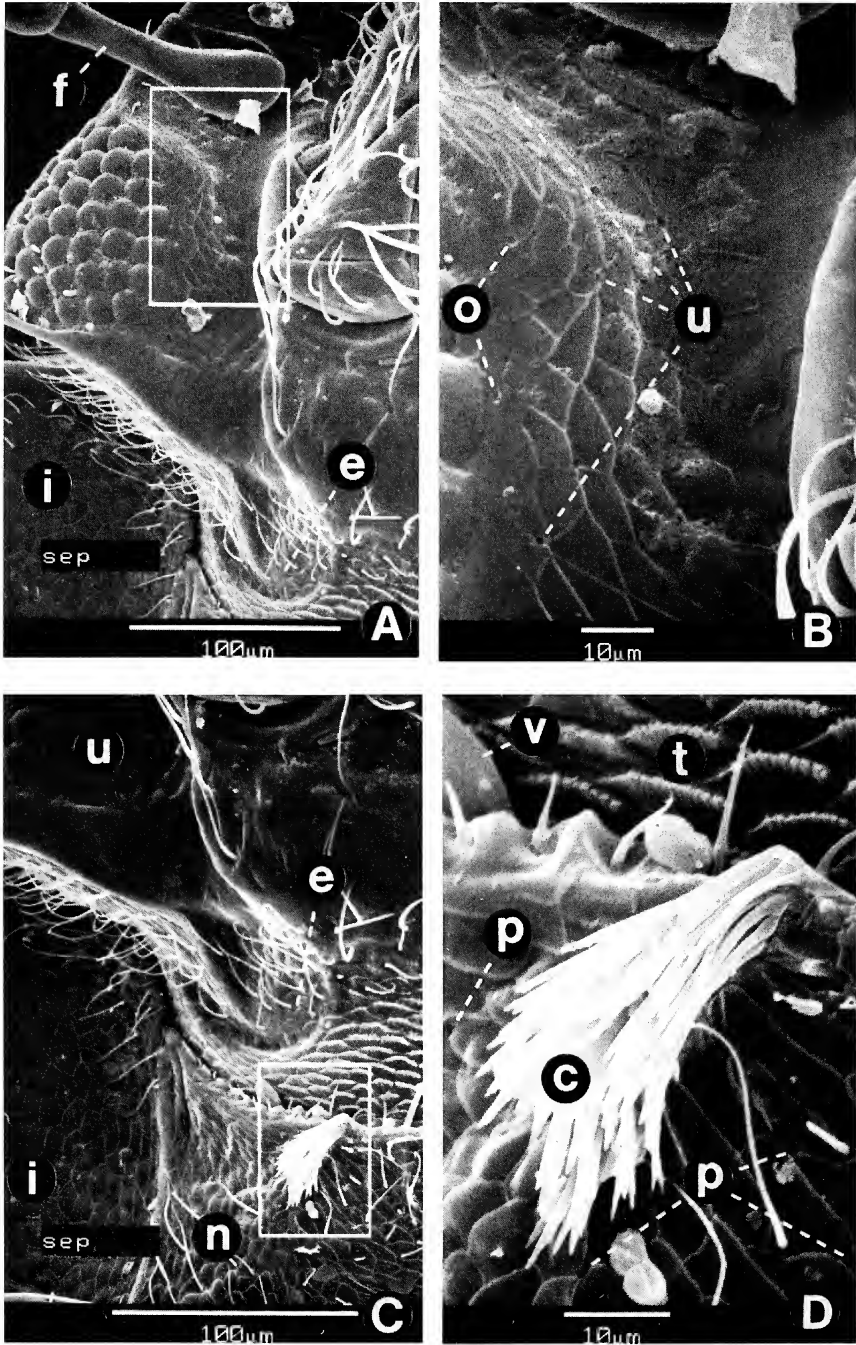


Fig. 60.—*Discozantaena* (undescribed species "SER," from South Africa). A. Head, ventral aspect of right side. B. Rectangular area of A, enlarged. C. Posterior area of head and adjacent prothorax, ventral aspect of right side. D. Rectangular area of C, enlarged. Structures: (c) antennal cleaner of prosternum, (e) genal antennal groove, (f) first article of antenna (remainder removed), (i) antennal pocket, (n) prosternum, (o) periocular exocrine pores, (p) exocrine pores of prosternum, (t) spiculate microreticulation, (u) exocrine pores of subocular antennal groove, (v) cervical sclerite.

primitive features, and lacks any synapomorphies that could be used to support placing members in other tribes. The geographical distribution of eastern and southern Africa, Madagascar, and southern India is consistent with an ancient Gondwanan (vicariance) distribution.

Members of this tribe have the following hypomerall features: (1) the antennal pocket is located in the anterior face of the hypomeron, at least partially closed ventrally by the anterior extreme of the large wet-hypomeron; (2) the setae on the anteroventral margin of the antennal pocket are moderately large, forming part of the pocket; (3) the nonmarginal setae on the anterior part of the wet-hypomeron are long and flexible; and (4) the hypomerall carina is not contiguous with the notosternal suture, hence the hypomerall hydrofuge attains the antennal pocket.

Like Hydraenidini, members of Madagastriini retain the plesiomorphic condition of 11 antennomeres, a postocular area generally lacking specialized sensilla (but see morphological section for details), and the pronotum has single (nonpaired) punctation. The last sternum, in females, is concealed beneath the sixth (visible) sternum, or only the distal margin exposed. The last sternum is also concealed in males of *Coelometopon*, but is exposed in *Davidraena* and (is huge) in *Madagaster* males. *Madagaster* and *Davidraena* have a band-like strip of reticulation at the medial margin of the antennal pocket, presumably an antennal cleaner.

Coelometopon appears to be a highly specialized member of this tribe, strongly built and with modifications, such as elevated eyes, resulting from selection for a hygropetric existence. Like *Hydraena*, the procoxae of *Coelometopon* are strengthened posteriorly by a joining of the pronotal postcoxal projections with posterolateral extensions of the prosternal process. However, this similarity is clearly convergent: transparency mounts show that in *Coelometopon* the tip of each postcoxal projection fits into a corresponding notch in the prosternal process, whereas the opposite is true in *Hydraena*.

Madagaster is related to other, as yet undescribed, genera from Madagascar. These genera are related to the Madagascar species *Gondraena franzi* and the Indian species *Gondraena indica* (Jäch 1994). *Gondraena* retains many primitive features that are basal for the tribe Madagastriini—including (a) primitive number of antennomeres (11), (b) a deep antennal pocket, (c) nervure intervals of elytra being more-or-less carinate and/or granulate, (d) ventrites 1–4 (entirely) and 5 (basally) with hydrofuge pubescence, and (e) aedeagus simple. A putative synapomorphy, not noted by Jäch (1994), for the type species from India and *Gondraena franzi* (and at least one other undescribed, closely related species in Madagascar) is the form of the antennal club: the last three meres are widened, and the last mere is shorter than the penultimate. Contrastingly, in *Madagaster* the antennal club is elongate, the last mere is longer than the penultimate, only the first two ventrites are entirely hydrofuge pubescent, and the aedeagus is very complex.

Madagaster, new genus

Type Species.—*Madagaster steineri*, new species.

Diagnosis.—Recognized by the 11 articles of the antenna (six + club); the slightly elevated eyes; the ocelli located closer to the midline than to the eyes; the short and robust maxillary palpi with length ratios of last three articles as three:three:four or one:one:one; the transverse, noncordiform pronotum with well-developed postocular emarginations; the elytra with four costae (on homo-

logues of intervals 3, 5, 7, and 9), some interrupted; the costae separated one from the other by three or four rows of punctures; the restricted abdominal hydrofuge pubescence; the apically enlarged and sexually dimorphic abdominal sterna; the very large wet-hypomeron; and the features of the postocular/hypomeral antennal pocket (see morphological section).

Description.—**Antennal pocket.** The hypomeral carina is well defined, angulate posteriorly, and becomes obsolete anteriorly at the antennal pocket. The bubble-hypomeron becomes increasingly narrow anteriorly, very narrow at slightly constricted entrance to antennal pocket.

The wet-hypomeron is very wide, becoming wider from posterior to anterior, reticulate, and with very sparse randomly distributed exocrine pores. Randomly distributed over the anterior fourth are about 12–16 hypomeral setae that are long and flexible, not basally widened. Hypomeral antennal pocket setae, stiffer than the hypomeral setae, about six in number, are submarginally located at the anteromedial angle of the wet-hypomeron. There are no organized clusters of exocrine pores or end-apparatus, and no secretion sulcus exists on the hypomeron. The antennal pocket is large and deep, narrowly opened ventrally. The presumed hypomeral antennal cleaner, a narrow band of scale-like reticulations, is located adjacent to the notosternal suture for its entire length.

A few pericocular exocrine pores are present. The subocular antennal groove is deep, its medial margin cariniform; a few exocrine pores (ca. five to ten) are present near the eye margin. The groove is microreticulate except for a small microspiculate area at posterior extreme. A postocular ridge, devoid of hydrofuge pubescence, has about 15 exocrine pores in the lateral part. Between the medial part of the postocular ridge and the eye is a bisinuate, longitudinal ridge bearing, on a prominence at its midlength, a cluster of prominent setae and exocrine pores. A low transverse carina, bearing tiny spicules, divides the area between the eye and the postocular ridge into a smooth anterior part (next to the eye) and a microreticulate posterior part. The postocular area, behind the postocular ridge, is clothed in hydrofuge, but lacks any specialized exocrine secretion delivery setae or sensilla.

Other characters. Size large, body about 2.50–3.00 mm long, form elongate oval, elytra posteriorly truncate, head not deflexed. Antennomeres 11 (six + club), third about as long as combined lengths of fourth to sixth. Maxillary palpi short, length ratios of articles two to four (last) as three : three : four or one : one : one. Eyes well developed, slightly elevated. Labrum set at angle to clypeus, apicomediaally deeply incised; anterior margin fringed with long setae. Clypeus anterior margin truncate, straight or slightly emarginate. Ocelli located closer to midline than to eyes, frons with short midlongitudinal sulcus between ocelli, and short oblique fovea at anterior margin of each ocellus; area behind and between ocelli with four low carinae. Pronotum with two narrowly separated, midlongitudinal foveae, anterior about twice as long as posterior, on each side with two oblique admedian and two sublateral foveae; area behind well-developed postocular emarginations and between anterior foveae elevated, tectiform; lateral depressions wide; lateral margin arcuate except weakly sinuate just before base. Anterior hyaline border extremely narrow, lateral and posterior absent. Elytra with four costae (on homologues intervals 3, 5, 7, and 9), some interrupted, the costae separated one from the other by three or four rows of punctures, punctures sometimes not serial. Prosternum in front of procoxae about as long as procoxal cavities, latter narrowly open behind. Intercostal sternite small, triangular. Legs moderately elongate, tarsi five–five–five. Abdominal sterna five and six enlarged, combined area subequal to or greater than that of first four sterna combined; in males fifth shorter than sixth, seventh very large and completely exposed; in females sixth longer than fifth, seventh very small, entirely retracted beneath sixth or just apical margin visible. Hydrofuge pubescence present on postocular area, bubble-hypomeron (except antennal pockets), notal postcoxal projections, mesosternum, metasternum, first two abdominal sterna, and lateral portions of third and fourth sterna.

Etymology.—Named in reference to the madicolous habitat and the greatly modified abdomen; gender feminine.

Madagaster steineri, new species

Type Material.—Holotype male: Madagascar, Antananarivo, Manakambahiny, in seepage over exposed granite cliff face, 12.i.1990, W. E. Steiner; deposited in the USNM. Fifteen paratypes, five with same data as holotype, ten with same data except date 15.ii.1990, (USNM, CMNH, MCZ).

Description.—Size (mm × 100; length/width): body (length to elytral apices) 299/140, head 51/84, pronotum 66/119, elytra 200/140. Clypeus and frons dull, with dual punctation comprised of very dense micropunctulate ground sculpture and less dense, large punctures, setae short. Labroclypeal suture

very deep, at midline with short longitudinal sulcus that nearly connects with similar sulcus at posterior of head. Short, deep sulcus in front of each ocellus. Pronotum with two narrowly separated midlongitudinal foveae, anterior twice as long as posterior; each side with two admedian and two sublateral foveae; lateral margin rounded. Pronotal disc rugosely punctate. Elytral suture costate in posterior. First two elytral "interval" costae (from suture) usually interrupted in two places (sometimes only once), third costa interrupted once, fourth costa not interrupted. Strongly sexually dimorphic: in males, maxillary palpomeres three and four very broad, flattened, and microreticulate on ventral surface, abdominal sterna two to four modified in midline, fifth with posteromedian triangular process, sixth retractable (over median portion) within fifth, seventh large and completely exposed, legs modified. Abdominal sterna five and six enlarged in both sexes, in male combined lengths of two to four equal one-half combined lengths of five and six.

Etymology.—I am pleased to dedicate this distinctive new species to Warren E. Steiner—friend, colleague, and field entomologist extraordinaire.

Discussion.—A figure of the male genitalia of *M. steineri*, and descriptions of additional new species in the genus will be given in a separate paper.

Genus *Davidraena* Jäch (Fig. 61–63)

Diagnosis.—Recognized by the 11 articles of the antenna (six + club), the ocelli located closer to the midline than to the eyes, the pronotum deeply excavate at the posterior angles (Fig. 61), the pronotum and elytra with granulate costae, the broad clypeus that forms a shelf under which the short, robust maxillary palpi are held, the abdominal hydrofuge pubescence restricted to the first two sterna, the very large wet-hypomeron, and the features of the postocular/hypomeral antennal pocket (see morphological section).

Description.—**Antennal pocket.** The hypomeral carina (j in Fig. 61–63) is well defined, angulate posteriorly, and becomes obsolete anteriorly at the antennal pocket. The bubble-hypomeron (h in Fig. 61–63) is very narrow for its entire length.

The wet-hypomeron (w in Fig. 61–63) is very smooth opposite the carina, reticulate anteriorly. The smooth area has very sparse (ca. 15) randomly distributed exocrine pores. Randomly distributed over the anterior fourth are about ten hypomeral setae that are long and flexible, not widened at the base, each with a wide socket. Hypomeral antennal pocket setae (a in Fig. 61–63), about 12 in number, are located on the anterior margin of the wet-hypomeron. There are no organized clusters of exocrine pores or end-apparatus, and no secretion sulcus exists on the hypomeron. The pronotal indentation (Fig. 61B), a deep notch located at the posterior margin of the wet-hypomeron, has a few exocrine pores located along its margin, and the "opening" of the indentation is "closed" by long setae. The antennal pocket (Fig. 63:i) is smooth, large, and deep, but narrowly opened ventrally. The hypomeral antennal cleaner (c in Fig. 61, 63), a narrow band of scale-like reticulations, is located adjacent to the notosternal suture, at the ventromedial margin of the antennal pocket. The inner margin of the antennal pocket bears a dorsomedial setal cluster (Fig. 61, 63D:b) that may be a site of exocrine secretion (substances present in one preparation [Fig. 63D:s] may be artifact).

A few periocular exocrine pores are present. The subocular antennal groove (Fig. 62:u) is deep, its medial margin cariniform, posteriorly the carina forms a prominent genal ridge (g in Fig. 61–63). A few exocrine pores (ca. five) are present in the subocular antennal groove. A postocular ridge (Fig. 62:z) bears a small setal cluster (Fig. 62:y) at the posterior extreme of the subocular groove. The postocular ridge is devoid of hydrofuge pubescence and has about 15 randomly distributed exocrine pores. The postocular area, behind the postocular ridge, is clothed in reticulate hydrofuge (Fig. 62:o), but lacks any specialized exocrine secretion delivery setae or sensilla.

Other characters. Size small, body about 1.35 mm long, form elongate oval, moderately convex, head not deflexed. Antennomeres 11 (six + club), third and sixth (first of club) moderately elongate, subequal to each other in length. Maxillary palpi very short and robust, length ratios of articles two to four (last) as four:three:five, located under shelf of clypeus. Features of antennal pocket as described in morphological section. Clypeus large, anterior margin wide, straight. Ocelli located closer to midline than to eyes, separated by low tumidity behind which are two short longitudinal carinae. Granule-based setae on margin of head and lateral margin of pronotum, except posteroangular excavations. Pronotal disc with two narrowly separated, parallel costae bearing granule-based setae, extended from base to apex. Pronotum transverse, lateral depressions and postocular emarginations well developed,

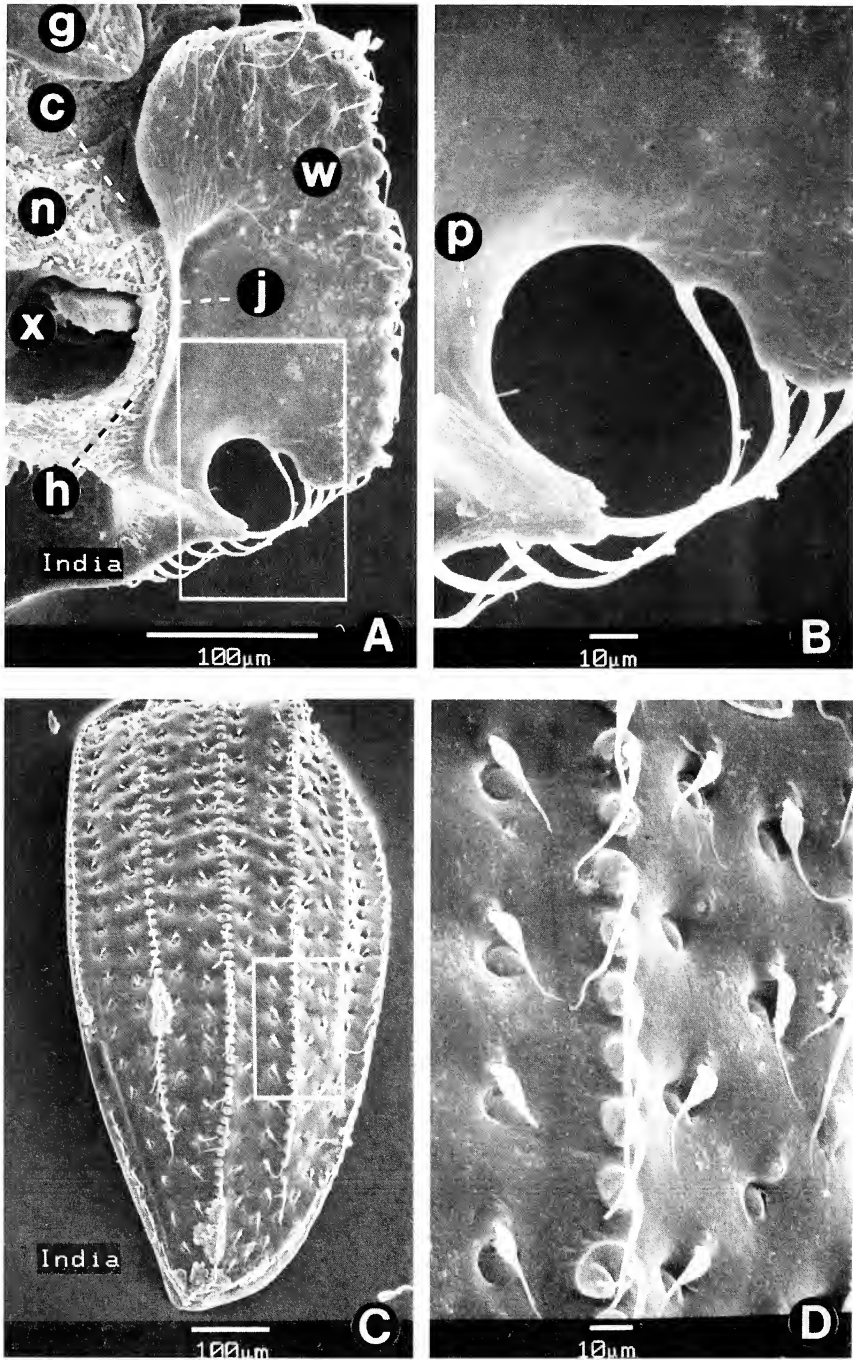


Fig. 61.—*Davidraena bacata*. A. Prothorax, ventral aspect of left side. B. Pronotal indentation (rectangular area of A, enlarged). C. Right elytron. D. Rectangular area of C, enlarged. Structures: (c) antennal cleaner of hypomeron, (g) genal ridge of subocular antennal groove, (h) hypomeral hydrofuge, (j) hypomeral carina, (n) prosternum, (p) exocrine pores at margin of pronotal indentation, (w) wet-hypomeron, (x) procoxal cavity.

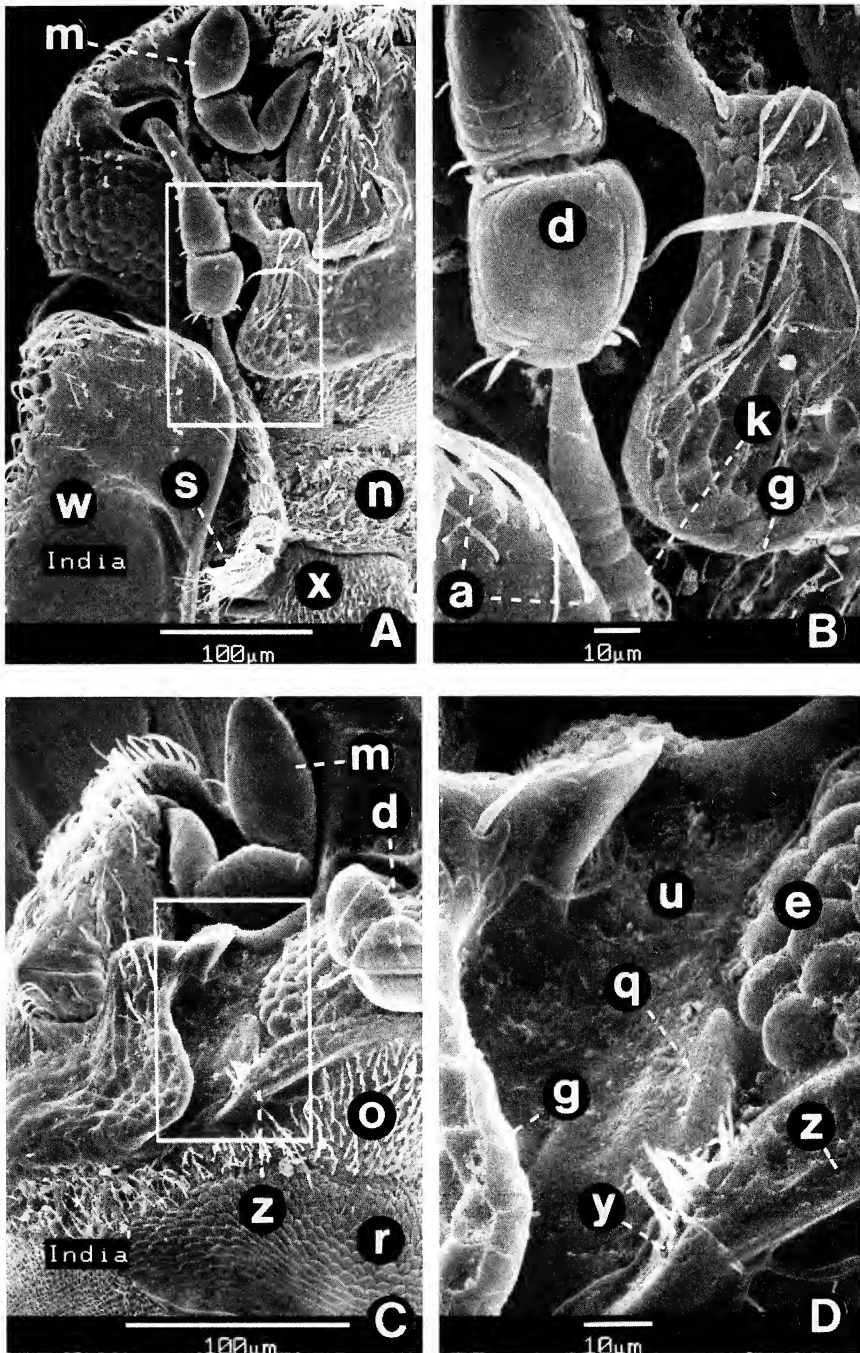


Fig. 62.—*Davidraena bacata*. A. Head and prothorax, ventrolateral aspect of right side. B. Rectangular area of A, enlarged. C. Head, posteroventral aspect of left side. D. Rectangular area of C, enlarged. Structures: (a) hypomerall antennal pocket setae, (d) second antennomere, (e) eye, (g) genal ridge of subocular antennal groove, (k) cupule article of antenna, (m) maxillary palpus, (n) prosternum, (o) postocular hydrofuge, (q) subocular ridge, (r) reticulation, (s) sensilla of antennal club, (u) subocular antennal groove, (w) wet-hypomeron, (x) procoxal cavity, (y) setal cluster of postocular ridge, (z) postocular ridge.

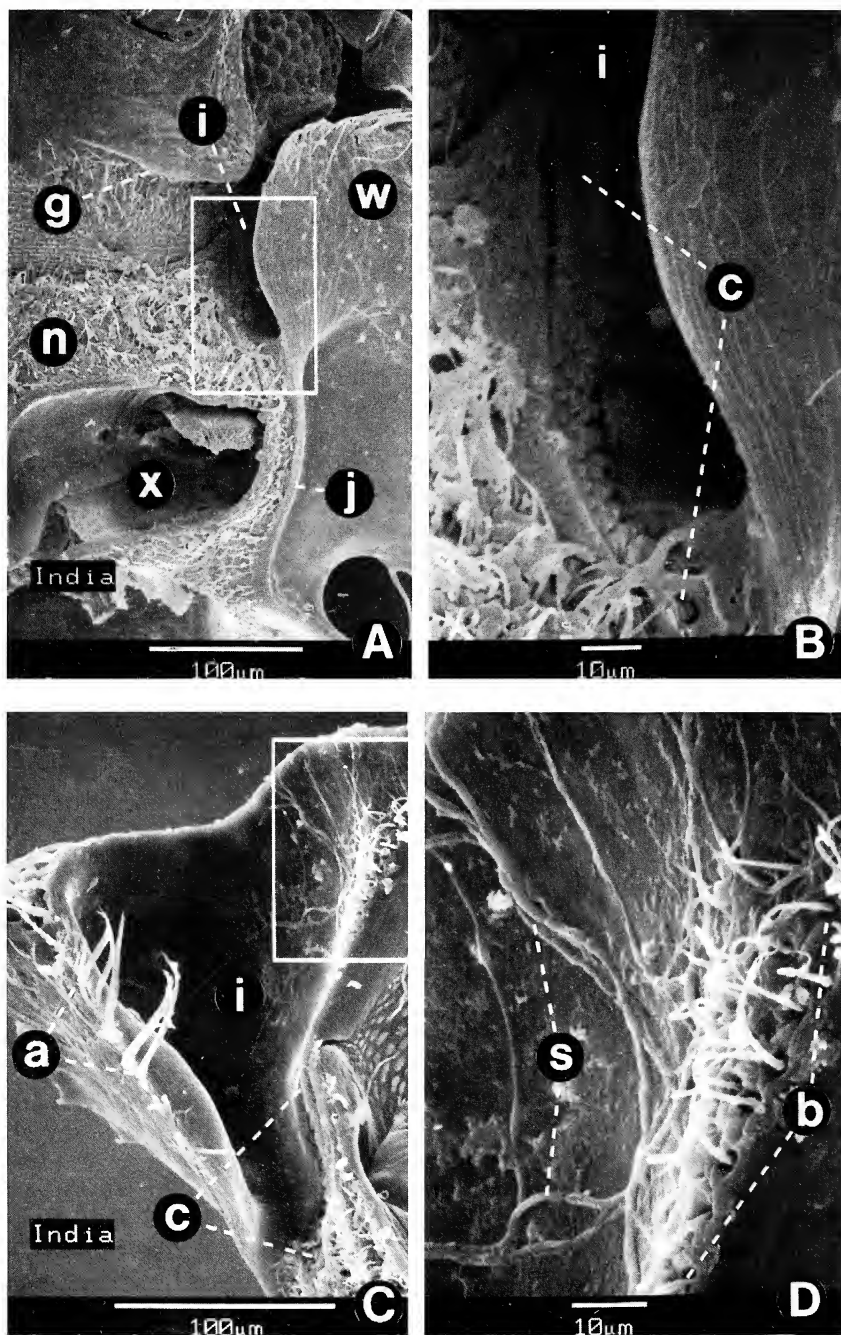


Fig. 63.—*Davidraena bacata*. A. Head and prothorax, ventral aspect of left side. B. Rectangular area of A, enlarged. C. Prothorax, anterior aspect of right side. D. Rectangular area of C, enlarged. Structures: (a) hypomer al antennal pocket setae, (b) dorsomedial setal cluster of antennal pocket, (c) antennal cleaner of hypomer on, (g) genal ridge of subocular antennal groove, (i) antennal pocket, (j) hypomer al carina, (n) prosternum, (s) presumed exocrine secretions, (w) wet-hypomer on, (x) procoxal cavity.

deep excavation at each posterior angle. Anterior hyaline border narrow, lateral and posterior absent. Elytra with ten series of punctures; sutural interval, even-numbered interseries, and lateral margin each costate and bearing unilinear row of granule-based setae. Prosternum shorter than procoxae, latter narrowly open behind. Intercostal sternite small, triangular. Legs short, tarsi very short, five–five–five. Hydrofuge pubescence present on postocular area, bubble-hypomeron (except antennal pockets), notal postcoxal projections, mesosternum, metasternum, and first two abdominal sterna. First two abdominal sterna short compared to other sterna.

Davidraena bacata, **new species**

(Fig. 58B, 60–63)

Type Material.—Holotype male: India, Kerala, Cardamon Hills, Muttapatti près Munnar, 1700m, 24.xi.1972, Besuchet, Löbl, Mussard; deposited in MHNG. Paratypes: ten specimens with same data (MHNG, MCZ).

Description.—Size (mm × 100; length/width): body 134/66, head 21/36, pronotum 33/60, elytra 87/66. Clypeus shining, very weakly microreticulate and bearing very small, sparse granules. Sculpture slightly more developed on frons, especially granule-based setae on median tumidity. Pronotum on each side with two oblique costae, parallel to one another, one extended from anterior margin to about midlength, the other extended from base to slightly past midlength; some areas between pronotal costae nonpunctate and strongly shining; posterolateral excavations semicircular and bearing overlapping setae at “entrance.” Elytra with noncostate intervals shining, punctures crescent-shaped, each bearing a basally enlarged seta at anterior margin. Metasternal disc very shallowly concave, hydrofuge pubescent. Length ratios of abdominal sterna two to four as one : one : one and one-half : two. Aedeagus (Fig. 58B) with well-developed parameres and lacking distal process or flagellum; length 0.15 mm.

Etymology.—Latin, *bacata* (adorned with pearls), in reference to the rows of elytral granules.

Genus *Coelometopon* Janssens

Discussion.—The following description is based on SEM and transparency mounts of *C. madidum* and two undescribed species from South Africa.

Description.—**Antennal pocket.** The hypomeral carina is distinct, angulate just before the postero-lateral angles; anteriorly becoming obsolete at the antennal pocket. The bubble-hypomeron becomes increasingly narrow anteriorly, very narrow at constricted entrance to antennal pocket, where antero-medial angle of wet-hypomeron is produced.

The wet-hypomeron is very wide in the anterior two-thirds, much narrower posteriorly, reticulate, almost lacking exocrine pores. Randomly distributed over the anterior fourth are about 12–16 hypomeral setae that are long and flexible, not basally widened; interspersed with these setae are much shorter, stout, arcuate setae similar to those on lateral margin. Hypomeral antennal pocket setae, about 12–15 in number, are located along the margin of the antennal pocket. There are no organized clusters of exocrine pores or end-apparatus, and no secretion sulcus exists on the hypomeron.

The antennal pocket is large and deep, narrowly opened ventrally, dorsally opened at well-developed postocular emarginations. A short, raised ridge or carina is present in the pocket, on the internal face of the hypomeron. The pocket is hydrofuge pubescent in a narrow band along the medial margin, and more extensively so at the dorsomedial area, otherwise the pocket is smooth and has very sparse exocrine pores. There appear to be no antennal cleaning structures in the pocket or on the prosternum.

Periocular exocrine pores are present. A sparse line of pores is present submarginally along the occipital carina. The subocular antennal groove is deep, its medial margin cariniform; a few exocrine pores are present in the groove and along its lateral margin. The groove is smooth except small spiculate area at the posterolateral extreme (i.e., the ventromedial extreme of the postocular area). The large postocular area is clothed in hydrofuge pubescence, but lacks any specialized exocrine secretion delivery setae or sensilla.

Tribe *Limnebiini* Mulsant

This group, formerly considered a subtribe (Perkins, 1981), comprises the genera *Limnebius* and *Laeliaena*. The tribe is characterized by (1) the slightly concave hypomeral shape, lacking a hypomeral carina, and having a short row of antennal pocket setae; (2) the smooth dorsal habitus; (3) the proportions of the antennae;

and (4) the shape and chaetotaxy of the mentum. The structure of the hypomeron and the mentum suggest a closer relationship with the Parhydraenini than with the Hydraenini.

Genus *Laeliaena* Sahlberg

Discussion.—This is a very rare genus, known only from a few specimens of two species from Turkestan and northern India. I have been able to study only a single transparency mount of an undescribed species from Nepal, plus one dry specimen of the type species *L. sparsa* J. Sahlberg. *Laeliaena* was proposed as a sister group to *Limnebius* by Perkins (1981:430), being similar in smooth dorsal habitus and in the form of maxillary palpi and antennae, but differing in having a less derived pronotal shape. This placement is strengthened by the hypomeral shape, and the separation of *Laeliaena* as a distinct genus is corroborated by the absence of a specialized ESDS.

Description.—**Antennal pocket.** The general shape of the hypomeron is very similar to that of *Limnebius* and, like that genus, a hypomeral carina is lacking and a short row of antennal pocket setae is present. However, there is no hypomeral glandular fovea, no exocrine gland cluster, and no distinct row of marginal setae bordering the hydrofuge hypomeron (i.e., no specialized ESDS). Additionally, the postocular area lacks antennal pocket setae.

Subfamily Prosthetopinae Perkins

The diagnostic features of the tribes and genera of this subfamily are given by Perkins and Balfour-Browne (1994). In contrast to the Ochthebiinae and Hydraeninae, characters of the antennal pocket and hypomeron are conservative in the Prosthetopinae. However, the subfamily is very diverse in other external features—consistent with the benthic microhabitat of many members (discussed in Perkins and Balfour-Browne, 1994).

Genus *Nucleotops* Perkins and Balfour-Browne (Fig. 64, 65)

Discussion.—The following description is based on SEM and transparency mounts of *N. nimbiceps*. Two new species of *Nucleotops* from South Africa will be described in a separate publication.

Description.—**Antennal pocket.** The hypomeral antennal pocket (Fig. 64:h, 65:h) is a very shallow depression on the anterior face of the hypomeron. In the aquatic genera the pocket is hydrofuge pubescent (Fig. 65A), whereas in the humicolous genus *Nucleotops* (Fig. 64C) the setae are spiniform. The pocket setae are contiguous with the pubescence of the prosternum, but not with that of the postcoxal projection.

The hypomeral carina (Fig. 64:e, 65:e) is well developed. Over its middle third the carina is contiguous with the notosternal suture, hence the hydrofuge pubescence of the antennal pocket and that of the postcoxal projection are not contiguous. Generally, a few (two to ten) exocrine pores are present along the part of the carina that borders the antennal pocket.

The wet-hypomeron (Fig. 64:w) is wide, varying from smooth to strongly microreticulate, and has random exocrine pores that vary in density and placement according to the species. There are neither organized clusters of pores, nor a secretion sulcus on the hypomeron. Antennal pocket setae are lacking, but in members of aquatic genera the anterior part of the wet-hypomeron has a few hypomeral setae (Fig. 65A:s) that vary in number (ca. four to ten) and length (very short to moderately long) depending on the taxon.

Periocular exocrine pores are present. The subocular antennal groove (Fig. 64:u, 65:u) is well developed, weakly microreticulate; along its medial margin are about five to ten randomly spaced exocrine pores. The lateral margin of the groove is cariniform in *Nucleotops* (Fig. 64A:r, 64B:r), smooth in the other genera (Fig. 65A).

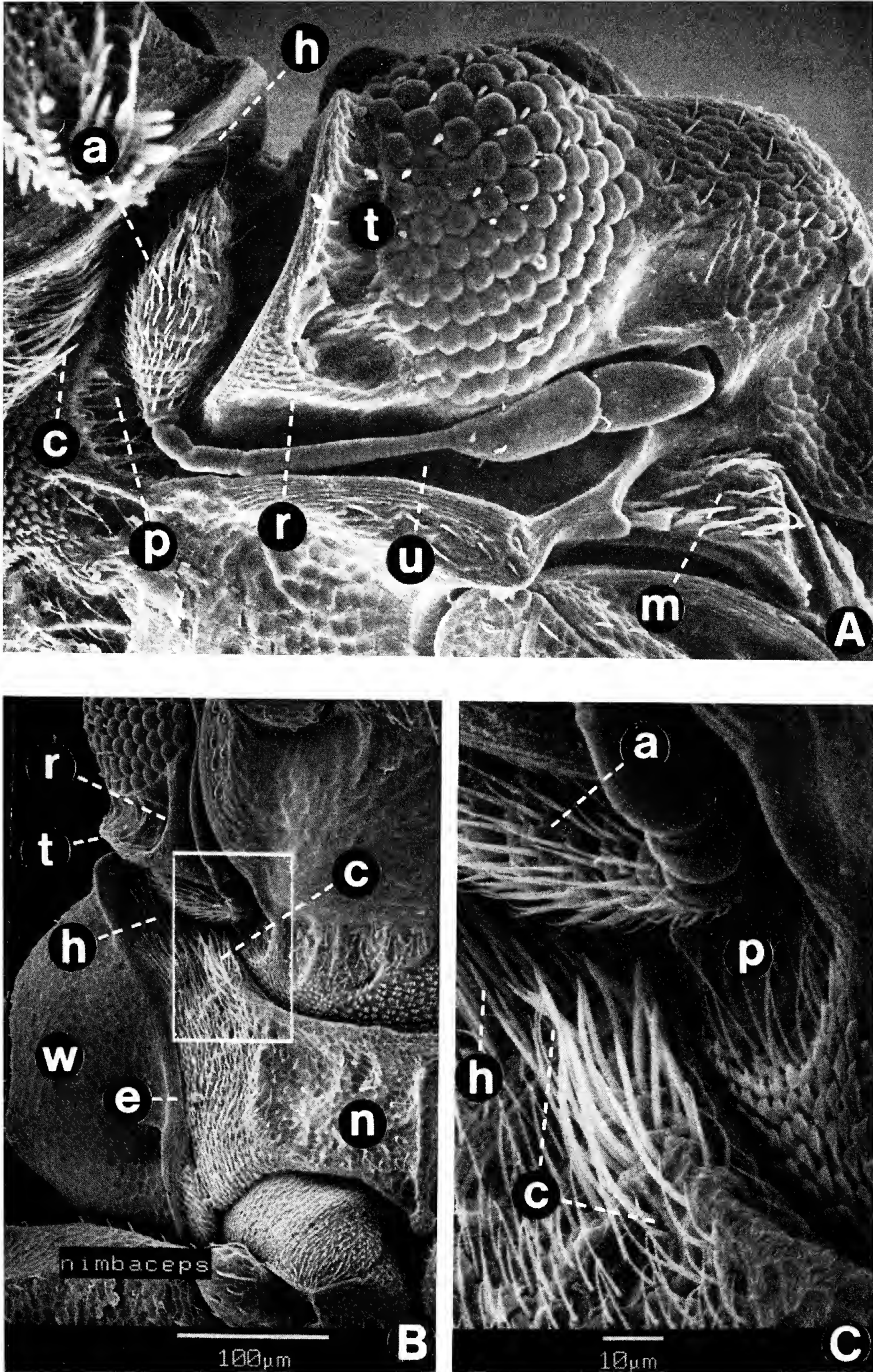


Fig. 64.—*Nucleotops nimbiceps*, head and prothorax, right side. A. Ventrolateral aspect. B. Ventral aspect. C. Detail of antennal cleaner and antennal club (rectangular area of B, enlarged). Structures: (a) antennifer, (c) prosternal antenna, (e) hypomeral carina, (h) antenna, (m) mandible, (p) postocular antenna, (r) lateral carina of antenna, (t) postocular carina, (u) subocular antenna, (w) wet-hypomeron.

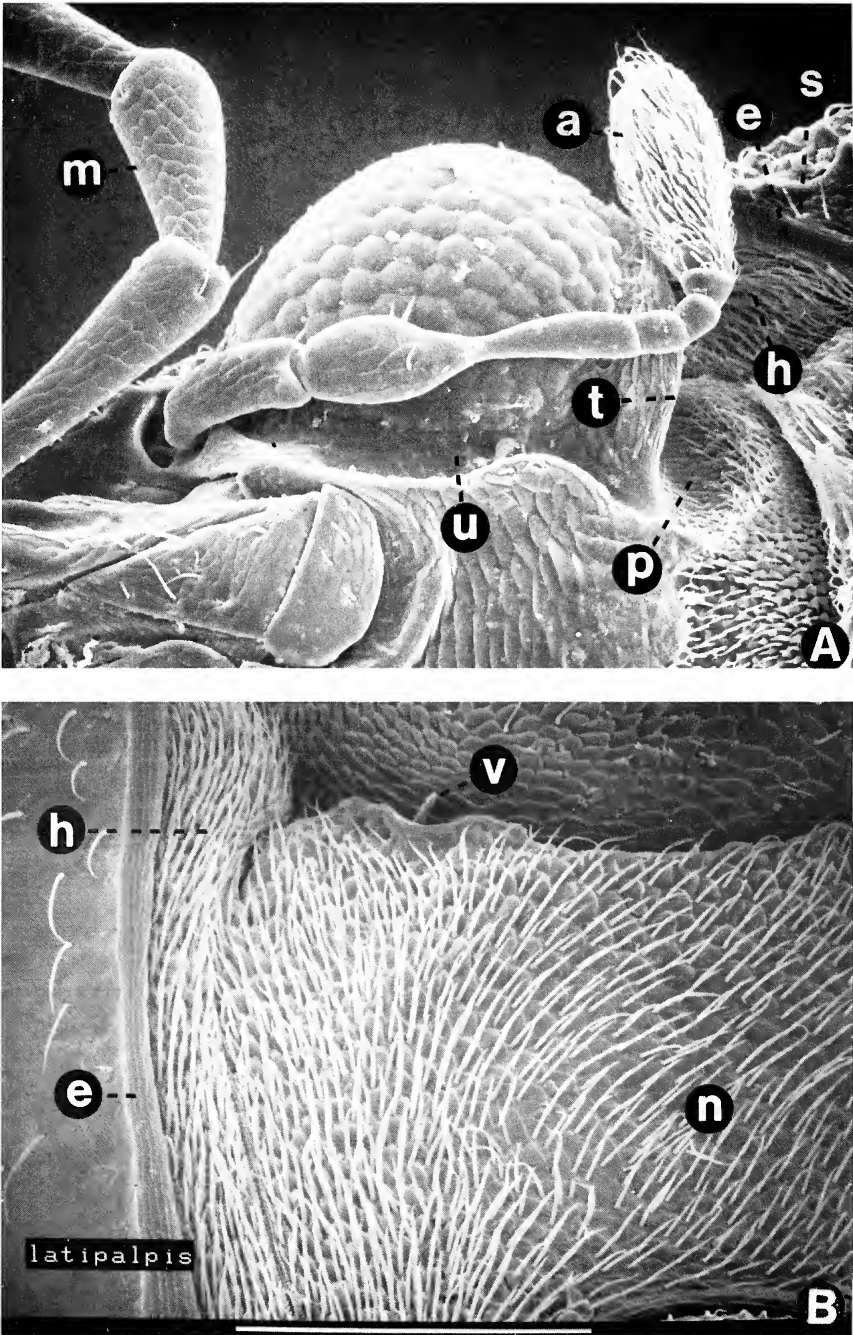


Fig. 65.—A. *Parasthetops nigratus*, ventral aspect of left eye and associated structures. B. *Podaena latipalpis*, venter of prothorax, right side. Structures: (a) antennal club, (e) hypomeral carina, (h) hydrofuge hypomeron, (m) maxillary palpus, (n) prosternum, (p) postocular antennal pocket, (s) hypomeral setae, (t) postocular carina, (u) subocular antennal groove, (v) cervical sclerite.

The postocular antennal pocket (Fig. 64:p, 65:p) is formed by the shallowly concave area behind the eye, and by a contiguous, small concavity on the gena. The pocket is bordered by a distinct postocular carina (Fig. 64:t, 65:t). Setae in the postocular part of the antennal pocket are of the hydrofuge type in the aquatic species, spiniform in *Nucleotops*. The remainder of the pocket (on the gena) may be reticulate and devoid of setae (Fig. 65A:p). The postocular area lacks any specialized exocrine secretion delivery setae or sensilla. In *Nucleotops*, the prosternal antennal cleaner (Fig. 64:c), a cluster of spiniform setae, is located on the anterior margin of the prosternum, adjacent to the antennal pocket.

Orchymontinae, new subfamily

This new subfamily is erected for the New Zealand endemic genera *Orchymontia* (type genus), *Podaena*, and *Homalaena*; these three genera are similar in the basic morphology of the postocular area and the hypomeron. Members of this subfamily are diagnosed by the following features: (1) hypomeral antennal pockets virtually absent, area clothed with hydrofuge; (2) gena with a shallow antennal pocket that is laterally limited by the horizontally oriented temporal lobe (hence head is not retractile to level of eyes); (3) dorsum of head at margin of eye with whip-like setae set in a reticulate field; (4) antennae retaining ancestral configuration of basal meres, apical (club) meres reduced, lacking hydrofuge pubescence; (5) last sternum, in females, concealed beneath the penultimate sternum; and (6) head with tentorium elongate and with laminatentoria not fused on meson (see discussion under Ochtheosini).

Derived features of this group include specialized supraocular whip-like setae set in a supraocular reticulate field (Fig. 67B:s, f; 69B:s, f); a reduced, entirely nonpubescent antennal club (Fig. 68A:a, 69D:a); and very dense, short, ventral vestiture (Fig. 70), probably plastron-forming. In some species the facets on the posterior part of the eye are reduced, forming a shallow ocular impression (Fig. 68B:i) that appears to conform to the path of movement of the antenna.

Genus *Podaena* Ordish (Fig. 66–70)

Discussion.—The following description is based on SEM preparations of *P. maclellani* (Zwick) and *P. latipalpis* Ordish, in addition to transparency mounts of *P. dentipalpis*, *Orchymontia ciliata* Ordish, and *Homalaena dispersa* Ordish.

Description.—**Antennal pocket.** A well-developed, rounded hypomeral carina (Fig. 66:e, 68:e) separates the wet- and the much smaller bubble-hypomeron. There is no antennal pocket. However, the bubble-hypomeron, a narrow band opposite the prosternum (Fig. 66E:h), widens anteriorly and continues into the area normally occupied by the antennal pocket (h in Fig. 66A, B, C).

The wet-hypomeron (Fig. 66A:w) is wide, smooth, and has sparse, random exocrine pores that vary in number according to the species (e.g., 10–20 in *O. spinipennis* and *P. dentipalpis*, 40–50 in *H. dispersa*). There are neither organized clusters of pores, nor a secretion sulcus on the hypomeron. Antennal pocket setae are entirely lacking.

Periocular exocrine pores are present. The subocular antennal groove (Fig. 67:u, 68:u) is well developed, weakly microreticulate; along its medial margin are about 10–14 random exocrine pores.

An oval, shallow, genal antennal pocket (Fig. 67:g, 68:g) is located at the end of the subocular antennal groove. The posterior part of the pocket has asperite hydrofuge and exocrine pores (Fig. 67D, 68D); the remainder of the ventral surface of the head lacks hydrofuge pubescence. A postocular ridge (r in Fig. 67–69) forms the lateral margin of the genal antennal pocket. The postocular area lacks any specialized exocrine secretion delivery setae or sensilla.

KEYS TO TAXA

The following diagnostic keys are given below: (1) Key to Subfamilies; (2) Key to Tribes and Genera of Hydraeninae; and (3) Key to Tribes, Subtribes, and

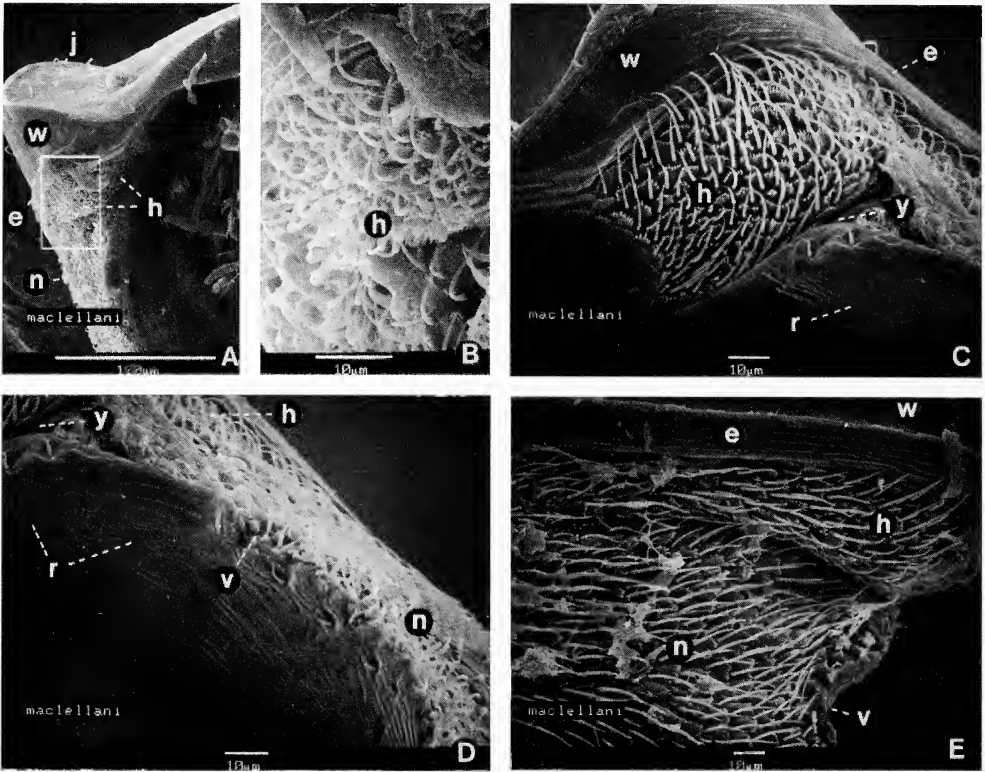


Fig. 66.—*Podaena maclellani*, prothorax. A. Anterior aspect of right side. B. Rectangular area of A, enlarged. C. Anteroventral aspect of hypomeron, left side. D. Cervical area of prosternum, left side. E. Hypomeron and prosternum, ventral aspect of right side. Structures: (e) hypomeral carina, (h) hypomeral asperite hydrofuge, (j) anterolateral area of pronotum, (n) prosternum, (r) reticulations of cervical area, (v) emargination of prosternum for cervical sclerite, (w) wet-hypomeron, (y) suture between prosternum and hypomeron.

Genera of Ochthebiinae. Keys to the genera of Orchymontinae are given by Ordish (1984), and to the taxa of Prosthetopinae by Perkins and Balfour-Browne (1994).

Key to Subfamilies

1. Hypomeral antennal pocket absent or at most a shallow depression on anterior face of hypomeron, lacking pocket-forming setae (Fig. 64B, 66A); antennal club reduced and/or articles tightly joined (Fig. 65A, 68A); ventral vestiture very short and dense (except some humicolous forms), often plastron-forming (Fig. 70A) 2
- 1'. Hypomeral antennal pocket varying from well-formed depression in anterior face of hypomeron (Fig. 15A) to more open concavity of hypomeron, either hydrofuge pubescent or with pocket-forming setae or hyaline ridges associated with bubble formation (Fig. 1A, 26A, 41A); antennal club longer, articles loosely articulated (Fig. 1A, 41A); ventral vestiture generally less dense, longer, hydrofuge (Fig. 1C) 3
2. Hypomeral antennal pockets absent, nonpubescent antennal club held in shallow, genal antennal pocket that is laterally limited by horizontally oriented temporal lobe (Fig. 68A); hypomeral carina separated from notosternal suture by bubble-hypomeron (Fig. 65B); head with supraocular whip-like setae set in reticulate field (Fig. 67A, B; 69A, B); mesosternal plaques absent Orchymontinae, new subfamily

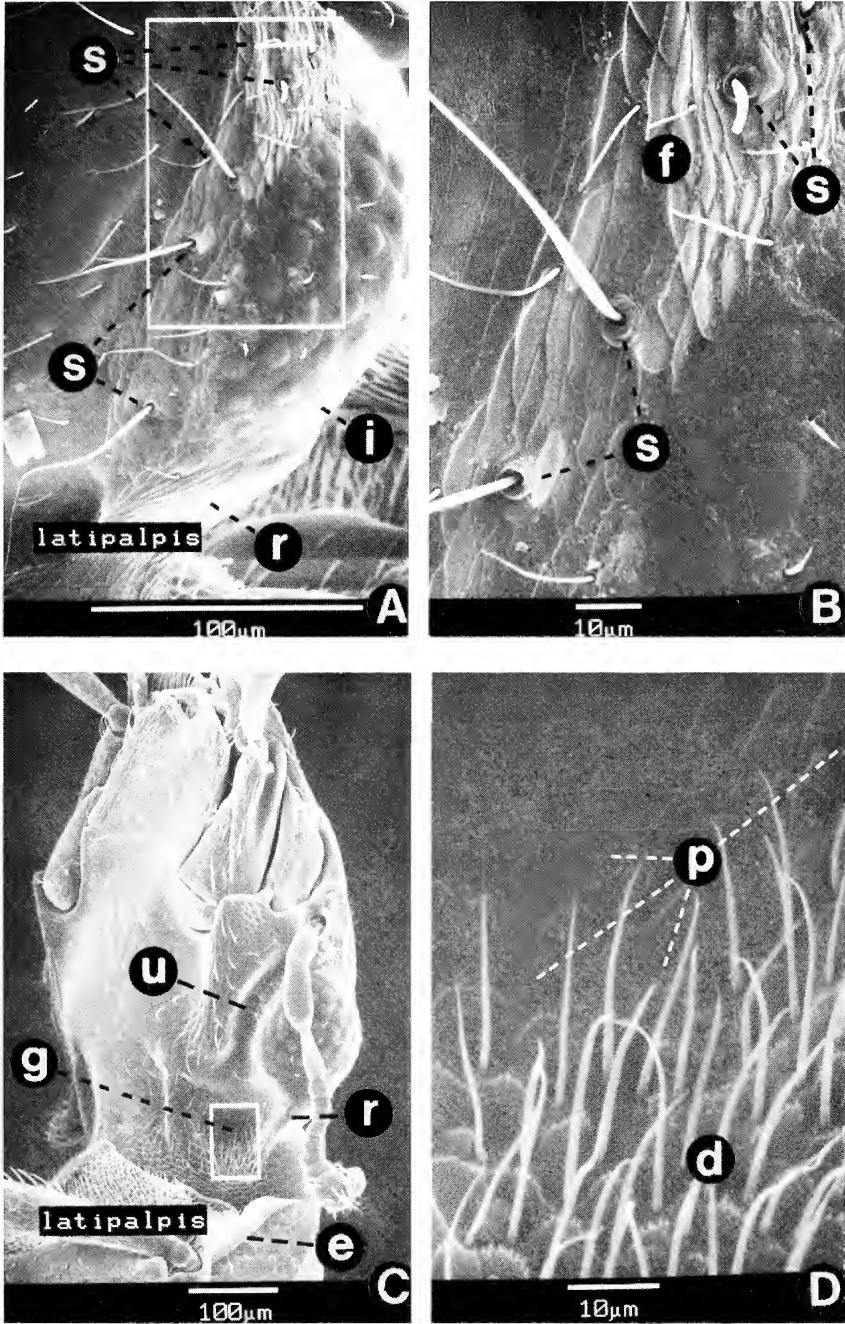


Fig. 67.—*Podaena latipalpis*, head. A. Supraocular area. B. Whip-like setae (rectangular area of A). C. Head, ventrolateral aspect. D. Genal antennal pocket (rectangular area of C). Structures: (d) asperite hydrofuge, (e) hypomer al carina, (f) supraocular reticulate field, (g) gular antennal pocket, (i) ocular impression, (p) exocrine pores of gular antennal pocket, (r) postocular ridge, (s) supraocular whip-like setae, (u) subocular antennal groove.

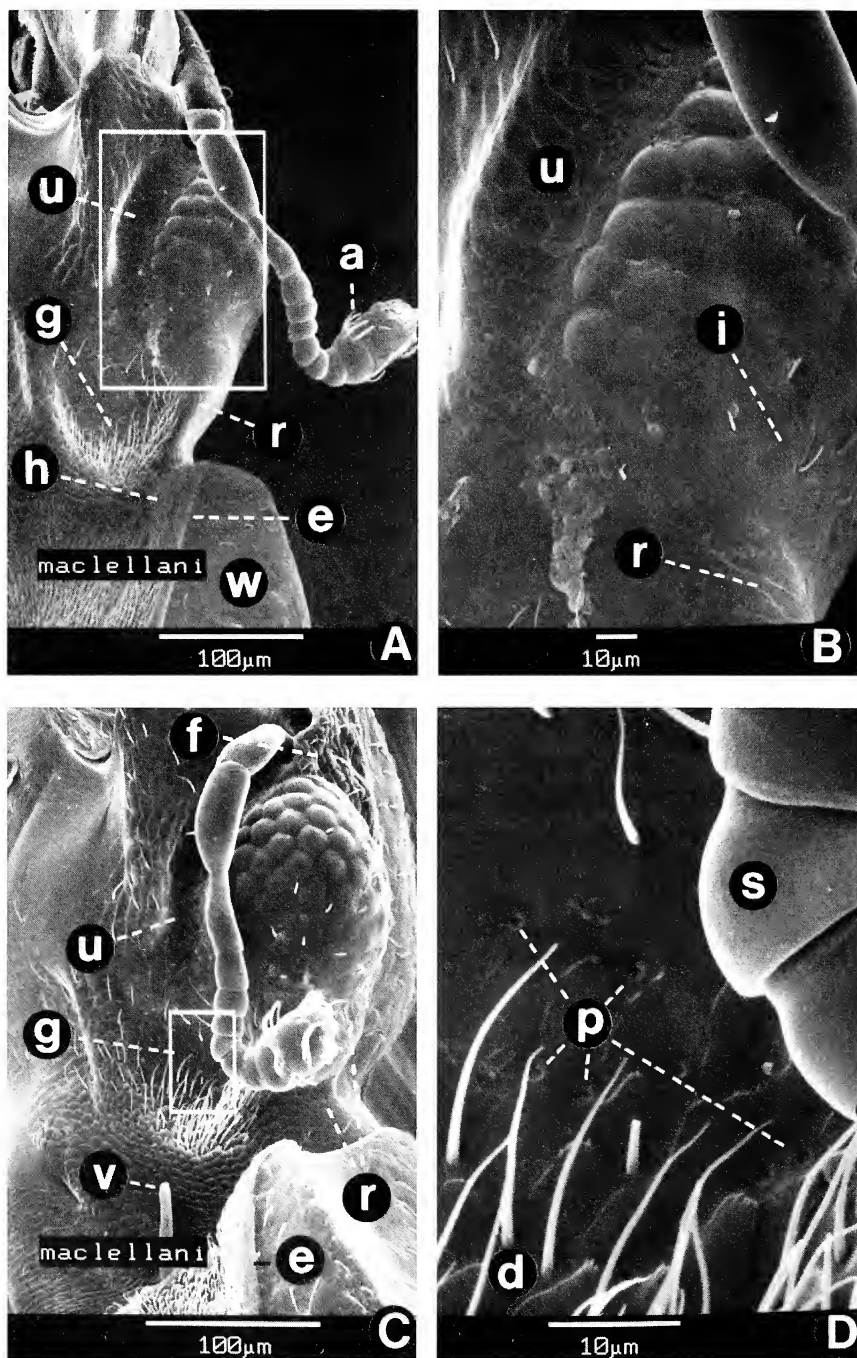


Fig. 68.—*Podaena maclellani*, head and prothorax, left side. A. Ventral aspect. B. Eye and adjacent structures (rectangular area of A). C. Ventrolateral aspect. D. Genal antennal pocket (rectangular area of C). Structures: (a) sensilla of antennal club, (d) asperite hydrofuge, (e) hypomerical carina, (f) supraocular reticulate field, (g) gular antennal pocket, (i) ocular impression, (p) exocrine pores of gular antennal pocket, (r) postocular ridge, (s) seventh antennomere, (u) subocular antennal groove, (v) cervical sclerite.

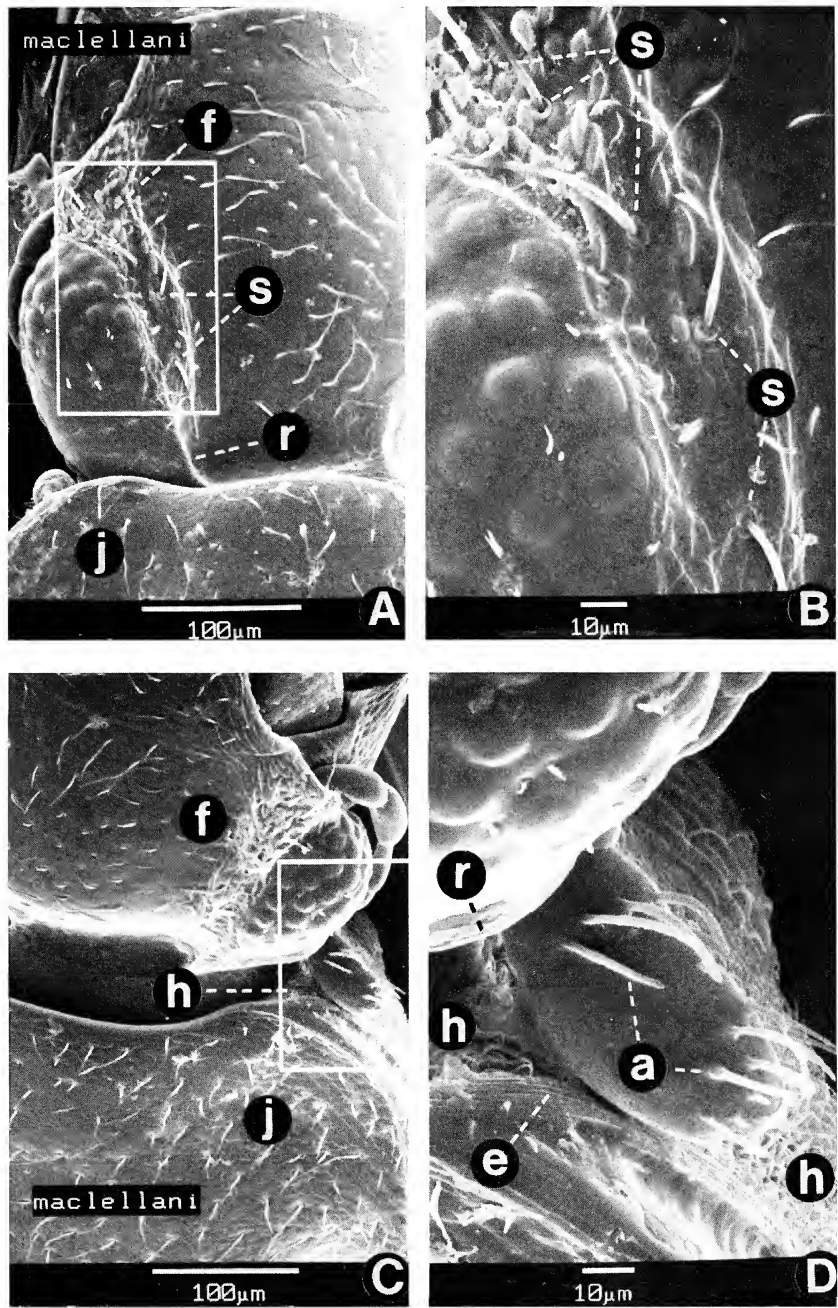


Fig. 69.—*Podaena maclellani*, dorsum of head and adjacent prothorax. A. Supraocular area. B. Whip-like setae (rectangular area of A). C. Oblique aspect. D. Antennal club and adjacent structures (rectangular area of C). Structures: (a) sensilla of antennal club, (e) hypomeran carina, (f) supraocular reticulate field, (h) hydrofuge hypomeran, (j) anterolateral angle of pronotum, (r) postocular ridge, (s) supraocular whip-like setae.

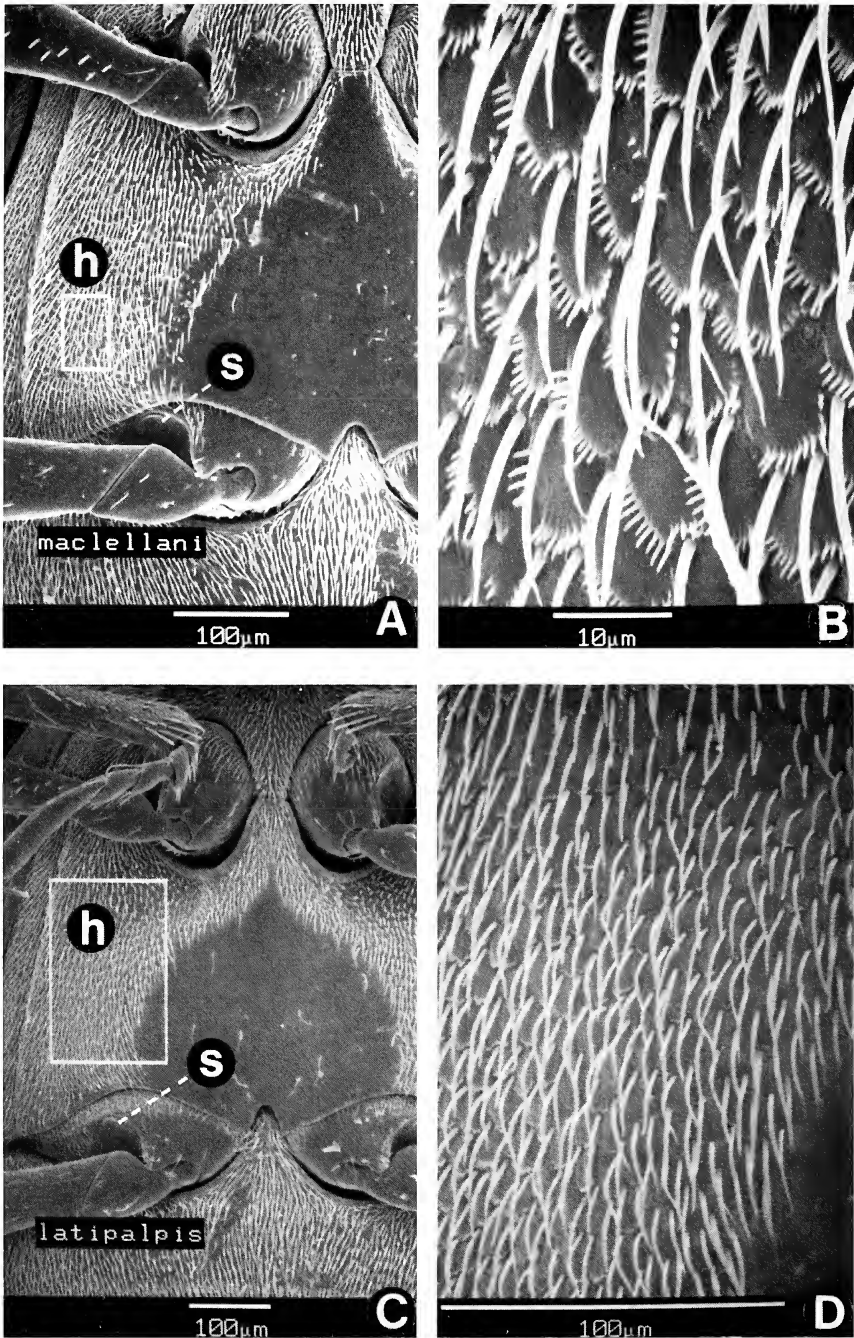


Fig. 70.—*Podaena*, metasternum and adjacent structures. A. *P. maclellani*. B. Vestiture (rectangular area of A). C. *P. latipalpis*. D. Vestiture (rectangular area of C). Structures: (h) hydrofuge or plastron vestiture, (s) metacoxal sensillum.

- 2'. Hypomer al antennal pockets very shallow, pubescent antennal club held behind eye, in post-ocular antennal pocket (Fig. 64A); hypomer al carina contiguous with median portion of notosternal suture, separating bubble-hypomeron into anterior and posterior parts (Fig. 64B); head lacking supraocular whip-like setae; mesosternum with submedian pair of plaques, sometimes joined to form inverted Y-shape Prostheto pinae Perkins
- 3. Hypomer al antennal pocket in ventral face of hypomeron, bordered medially by notosternal suture (Fig. 1A, 42A, 44A, 48A); penultimate maxillary palpomere more robust and longer than ultimate (Fig. 30C); specialized ESDS gland concentration in head Ochthebiinae Thomson
- 3'. Hypomer al antennal pocket in anterior face of hypomeron, generally anterior to most of notosternal suture, with lateral portion of pocket formed by extensive wet-hypomeron (Fig. 18A, 52C, 54A, 63A), or specialized hypomer al antennal pocket setae (Fig. 26A, 57A); penultimate maxillary palpomere neither longer than nor more markedly robust than ultimate; specialized ESDS gland concentration in prothorax Hydraeninae Mulsant

Key to Tribes and Genera of Hydraeninae

- 1. Hypomer al antennal pocket formed by stiff, arcuate hap-setae (Fig. 26A:e, 57A:a; secondarily reduced in *Discozantaena*); anterior part of wet-hypomeron not enclosing antennal pocket (except *Pneuminion*) 2
- 1'. Hypomer al antennal pocket, at anterior extreme, formed by wet-hypomeron, which may bear hap-setae on medial margin (Fig. 10A, B; 18A; 54A; 61A) 7
- 2. Hypomeron slightly to markedly concave, lacking hypomer al carina, anteriorly with short row of hap-setae (Fig. 26A); dorsum smooth, quite evenly convex; pronotal foveae absent or indistinct, punctures not paired; antenna with nine articles (four + club), second article slightly longer than first, about twice length of second; antennal club with each article slightly larger than preceding; prosternum lacking antennal cleaner (Limnebini Mulsant) 3
- 2'. Hypomeron not concave, except at antennal pocket, with or without hypomer al carina (Fig. 57C); dorsum not evenly convex, pronotum with distinct impressions and paired punctures; antenna with either ten or 11 articles (five or six + club), second article shorter than first, not twice as long as third; antennal club with second article slightly smaller than first; prosternum anterolaterally with cluster of sharp spines (antennal cleaner?) (Fig. 57A:c, 59B: c; Parhydraenini new tribe) 4
- 3. With ESDS components: hypomer al glandular fovea, marginal setae of hydrofuge hypomeron, and postocular antennal pocket setae (Fig. 26, 27); pronotum widest basally, body contour uninterrupted; antennal club more loosely articulated, each article larger than preceding; aquatic species; nearly cosmopolitan *Limnebius* Leach
- 3'. Lacking ESDS components cited above; pronotum narrowed basally, body contour interrupted between prothorax and elytra; antennal club with last three articles tightly joined to form oval outline distinctly larger than basal two articles; aquatic species; Turkestan, India, and Nepal *Laeliana* Sahlberg
- 4. Anterior extreme of wet-hypomeron enclosing part of antennal pocket; pronotum anterior margin with distinct postocular emarginations; antenna with 11 articles (six + club); aquatic species; South Africa *Pneuminion* n. gen.
- 4'. Wet-hypomeron not enclosing antennal pocket (Fig. 57A); pronotum anterior margin lacking postocular emarginations; antenna with ten articles (five + club) 5
- 5. Hypomer al antennal pocket bordered posteriorly with sparse, indistinct, flexible setae that lie on cuticle in dry specimens (Fig. 59A:a); pronotum explanate, widest slightly behind middle, then markedly attenuate to posterolateral angles, each of which is produced in small acute point; explanate margin of elytron very wide, in habitus view concealing tibiofemoral articulation; maxillary palpi and tarsi very short; humicolous species; South Africa *Discozantaena* Perkins and Balfour-Browne
- 5'. Hypomer al antennal pocket bordered posteriorly with long, stiff, arcuate setae (Fig. 57D:a); pronotum widest near midlength, posterolaterally subrectangulate; maxillary palpi and tarsi of various lengths 6
- 6. Hypomer al carina absent; maxillary palpus large, as long as antenna, apical article wide, inner surface arcuate at base; aedeagus with long terminal flagellum and very short parameres; aquatic species; South Africa *Protozantaena* n. gen.

- 6'. Hypomer al carina separating wet- and bubble-hypomeron (Fig. 57C:b); maxillary palpi of various lengths, not shaped as above; aedeagus not as above; aquatic and humicolous species; eastern and southern Africa *Parhydraena* Orchymont
7. Prosternal intercoxal process expanded laterally behind procoxae, closing procoxal cavities by interlocking with postcoxal pronotal projections (Fig. 52C), tip of each lateral projection of intercoxal process fitting into small notch in corresponding postcoxal pronotal projection; second article of maxillary palpus elongate and slender (Fig. 15C); last sternum of females with pair of sensory clusters; anterior part of wet-hypomeron lacking elongate flexible setae; antenna with nine or ten articles (four or five + club; Hydraenini Mulsant) 8
- 7'. Prosternal intercoxal process not expanded laterally behind procoxae (Fig. 63A), or if procoxal cavities closed (*Coelometopon*), then each lateral projection of intercoxal process with notch into which fits corresponding tip of postcoxal pronotal projection; second article of maxillary palpus not elongate and slender; last sternum of females lacking pair of sensory clusters; anterior part of wet-hypomeron with elongate flexible setae (Fig. 54A:a, 61A); antenna with 11 articles (six + club) 9
8. Hypomeron with ESDS sulcus; bubble-hypomeron not lobe-shaped anteriorly; antennal pocket with antennal cleaner (Fig. 12A, 13A, 15A); gena with stiff gap-setae (Fig. 19A:b); labrum and mandible with interlocking mechanism; mentum with apicomedian process; antenna with nine articles (four + club); aquatic species; cosmopolitan *Hydraena* Kugelann
- 8'. Hypomeron lacking ESDS sulcus; bubble-hypomeron lobe-shaped anteriorly (Fig. 52C); antennal pocket lacking antennal cleaner; gena with elongate, flexible setae (Fig. 53B:g), lacking stiff gap-setae; labrum and mandible lacking interlocking mechanism; mentum with apicomedian notch; antenna with ten articles (five + club); aquatic species; Venezuela *Adelphydraena* Perkins
9. Hypomer al carina contiguous with (or nearly so) notosternal suture (Fig. 54B), hydrofuge pubescence restricted to postcoxal pronotal projection; setae on margin of wet-hypomeron at opening to antennal pocket very small, not pocket-forming; last sternum of female exposed and bearing setae; South America (Hydraenidini Perkins) 10
- 9'. Hypomer al carina separated from notosternal suture by narrow band of hydrofuge pubescence that is continuous with pubescence of postcoxal pronotal projection (Fig. 61A); setae on margin of wet-hypomeron larger, pocket-forming (Fig. 62B:a); last abdominal sternum of female concealed beneath sixth, or only distal nonsetose margin exposed; southern Africa, Madagascar, and India (Madagastrini new tribe) 12
10. Antennal pocket open dorsolaterally (Fig. 55); abdomen with first and lateral thirds of second sterna hydrofuge pubescent, remainder with sparse, more robust setae; elytra posteriorly narrowed and transversely convex; aedeagus lacking parameres; aquatic species; Ecuador *Haptaenida* n. gen.
- 10'. Antennal pocket not open dorsolaterally; abdominal pubescence not as above; elytra not as above; aedeagus with parameres, although sometimes reduced 11
11. Pronotum subcordate, sides sinuate near posterior angles; elytra with serial rows of punctures in sulcate impressions, intervals costate or subcostate; aedeagus with left paramere originating near apex, right paramere absent or reduced to small spike near apex; hygropetric; South America *Parhydraenida* J. Balfour-Browne
- 11'. Pronotum with sides straight near posterior angles; elytra with serial rows of punctures not in sulcate impressions, intervals flat or slightly rounded; aedeagus with both parameres elongate, originating near base; aquatic; Chile *Hydraenida* Germain
12. Head with frons concave between protuberant and elevated eyes; hypomer al antennal pocket lacking band-like strip of reticulation at medial margin; antenna with combined lengths of first two articles slightly greater than remainder of antenna; hygropetric; eastern and southern Africa *Coelometopon* Janssens
- 12'. Head not as above; hypomer al antennal pocket with band-like strip of reticulation at medial margin (antennal cleaner?; Fig. 63B:c); antenna with combined lengths of first two articles much shorter than remainder of antenna 13
13. Pronotum deeply excavate at posterior angles (Fig. 61A); elytra with ten series of punctures; elytra with sutural interval, even-numbered interseries and lateral margin each costate and bearing unilinear row of granule-based setae (Fig. 61C); humicolous; southern India *Davidraena* Jäch

- 13'. Pronotum lacking excavations at posterior angles; elytra with four costae (on homologues of even-numbered intervals), some interrupted, costae separated one from the other by three or four rows of punctures, punctures sometimes not serial; hygropetric; Madagascar *Madagaster* n. gen.

Key to Tribes, Subtribes, and Genera of Ochthebiinae

1. Antenna with 11 articles; lacinia bearing many brush-like, slender setae; maxillary palpi arching, apex directed ventrad, second article arcuate; ocelli located near midline of frons; tentorium lacking wall-like anterior thickening; antennal pockets lacking specialized ESDS structures; fungicolous species; southern Chile (Ochtheosini new tribe) . . . *Ochtheosus* n. gen.
- 1'. Antenna comprised of nine or eight articles; lacinia bearing enlarged, stout apical teeth; maxillary palpi not distinctly arching ventrad; ocelli more widely separated, not located near midline of frons; tentorium with wall-like anterior thickening with a central "foramen"; antennal pockets with or without specialized ESDS structures (Ochthebiini Thomson) 2
2. Abdomen (both sexes) with seventh (last) sternum concealed beneath sixth, or just distal margin exposed, with micropores, but lacking setae; aedeagus lacking parameres, main-piece not markedly arcuate basally; last abdominal sternum of males without strut; antennal club not set at an angle to preclub (morphological sixth) article, latter not cupuliform, or only very slightly so; antennal pocket without specialized ESDS structures (Meropathina new subtribe) 6
- 2'. Abdomen (both sexes) with seventh (last) sternum exposed and bearing setae; aedeagus with parameres, main-piece basally arcuate; last abdominal sternum of males with strut; antennal club set at an angle to cupuliform preclub (morphological sixth) article, or articulating with latter such that an angle can be formed; antennal pocket with or without specialized ESDS structures 3
3. Prothorax without wet-hypomeron; hypomeral antennal pocket entirely microreticulate; post-ocular area without specialized ESDS structures; profemur without distal spine cluster 4
- 3'. Prothorax with wet-hypomeron delimited medially by hypomeral hyaline border; hypomeral antennal pocket not entirely microreticulate; postocular area with specialized ESDS structures; profemur with or without distal spine cluster 5
4. Prothorax without hypomeral hyaline border; head without transgenal sulcus; antenna with second article tapering distally, third article distally enlarged, shorter than second; eyes reduced; aquatic, intertidal; Japan and western U.S.A. (Neochthebiina new subtribe) *Neochthebius* Orchymont
- 4'. Prothorax with hypomeral hyaline border at lateral margin of hypomeron, horizontally oriented; head with transgenal sulcus; antenna with second article truncate distally, third article narrow throughout, longer than second; eyes not reduced; aquatic; Nepal (Protochthebiina new subtribe) *Protochthebius* n. gen.
5. ESDS with smooth postocular secretion delivery (psd-) shelf and psd-setae with brush-like tips; hypomeral hyaline border wide at anterior extreme; hypomeral antennal pocket (hap-) setae short relative to width of hypomeral hyaline border; aquatic; Palearctic and Nearctic (Enicocerina new subtribe) *Enicocerus* Stephens
- 5'. ESDS with secretion delivery area consisting of sulcus (either postocular or transgenal) or spiculate area; psd-setae of various forms; hypomeral antennal pocket (hap-) setae of variable length, usually much longer than anterior extreme of hypomeral hyaline border (Ochthebiina Thomson) 8
6. Hypomeral antennal pocket shallow, hydrofuge pubescent except narrow lateral marginal band (Fig. 41); postocular area lacking carina; antenna with second article ovoid, not cupuliform; metasternum reduced, entirely hydrofuge pubescent; dorsum with strong recumbent setae; terrestrial, coastal (porous rock, bird nests, grass tussocks, under stones); New Zealand, sub-Antarctic islands and islands at southern tip of South America . . . *Meropathus* Enderlein
- 6'. Hypomeral antennal pocket deeper, hydrofuge pubescence restricted to about medial half (Fig. 42A:i, 44A:i); postocular carina or ridge distinct; antenna with second article large, distal end cupuliform (Fig. 43C:y); metasternum not reduced, with large median glabrous area; dorsal vestiture various 7
7. Wet-hypomeron anteriorly enclosing part of antennal pocket, margin bearing large, strong setae (two or four; Fig. 44:g, 45:g); hypomeral carina distinct, dividing wet- and bubble-

- hypomeron (Fig. 44C); venter of head lacking longitudinal ridges; prosternum lacking antennal cleaner; metasternum with large median, convex glabrous area; dorsal vestiture various; aquatic, splash zone, and hygropteris; eastern Australia and Tasmania *Tympanogaster* Janssens
- 7'. Hypomeron entirely concave anteriorly, lacking wet-hypomeron delimited by hypomeral carina (Fig. 42A:i); venter of head with three, longitudinal submental ridges (Fig. 43A:m); prosternum with two clusters of spines (antennal cleaner?; Fig. 43B:a); metasternum with midlongitudinal impression; dorsum with strong, recumbent setae; humicolous; southwestern Australia *Tympalopatrum* n. gen.
8. Head with transgenal secretion sulcus, cuticle raised on each side of sulcus to form transgenal ridge (Fig. 40:z); psd-setae elongate, with tapering tips; hh-border large anteriorly, contacting psd-setae (Fig. 40:o); hap-setae not extended beyond margin of hh-border; posterior border of pronotum arcuate, without distinct posterior angles; hh-border contiguous with ph-border, lh-border absent; profemur without distal spine cluster; meso- and metacoxae transversely well separated (in derived condition); aquatic, coastal rockpools; southern Australia, northern Tasmania *Hughleechia* Perkins
- 8'. Head without transgenal secretion sulcus; psd-setae various; prothorax with hh- and lh-borders in addition to ah- and ph-borders; profemur with distal spine cluster; pronotum with distinct posterior angles 9
9. Venter of head near posteroventral angle of eye with strongly microreticulate shelf that terminates in spiculate secretion area (Fig. 38:z, 39:z); plumose secretion delivery setae, each with multiply branched tips, adjacent to spiculate secretion area (Fig. 38:a, 39:a); hap-setae short, extending only slightly beyond margin of lh-border (Fig. 38A:g); aquatic; eastern Australia *Gymnanthelium* n. gen.
- 9'. Head at posteroventral angle of eye with psd-sulcus (e.g., Fig. 29:c); psd-setae of various forms, but not plumose 10
10. Psd-sulcus continuous with transgenal ridge (Fig. 37:z); psd-setae short, slightly widened from base to apex, flattened, and apically fringed (Fig. 37:a); hap-setae about twice as long as width of hh-border (Fig. 37:g); pronotum with two deep transverse grooves, one in front of and one behind middle, connected by median longitudinal groove; pronotal anterior angles lobate; vestiture of ventrites consisting of hydrofuge setae and stiff, erect spines; aedeagus with gonopore at apex of mainpiece, not on preapical distal piece; body size very small; aquatic; Old World *Aulacochthebius* Kuwert
- 10'. Head without transgenal ridge; psd-setae elongate, tapering to pointed apices, often flattened; hap-setae elongate, contacting psd-setae (e.g., Fig. 1A, 2A); pronotum not as above; body size usually larger 11
11. Aedeagus with gonopore at apex of bifurcate main-piece; pronotal anterior angles usually lobate; vestiture of ventrites consisting of hydrofuge setae and stiff, erect spines; aquatic; North and South America and Australia *Gymnochthebius* Orchymont
- 11'. Aedeagus with gonopore at apex of mobile distal piece that originates preapically on main-piece; pronotal anterior angles not lobate; vestiture of ventrites hydrofuge setae without spines; aquatic; nearly cosmopolitan *Ochthebius* Leach

CONCLUSIONS

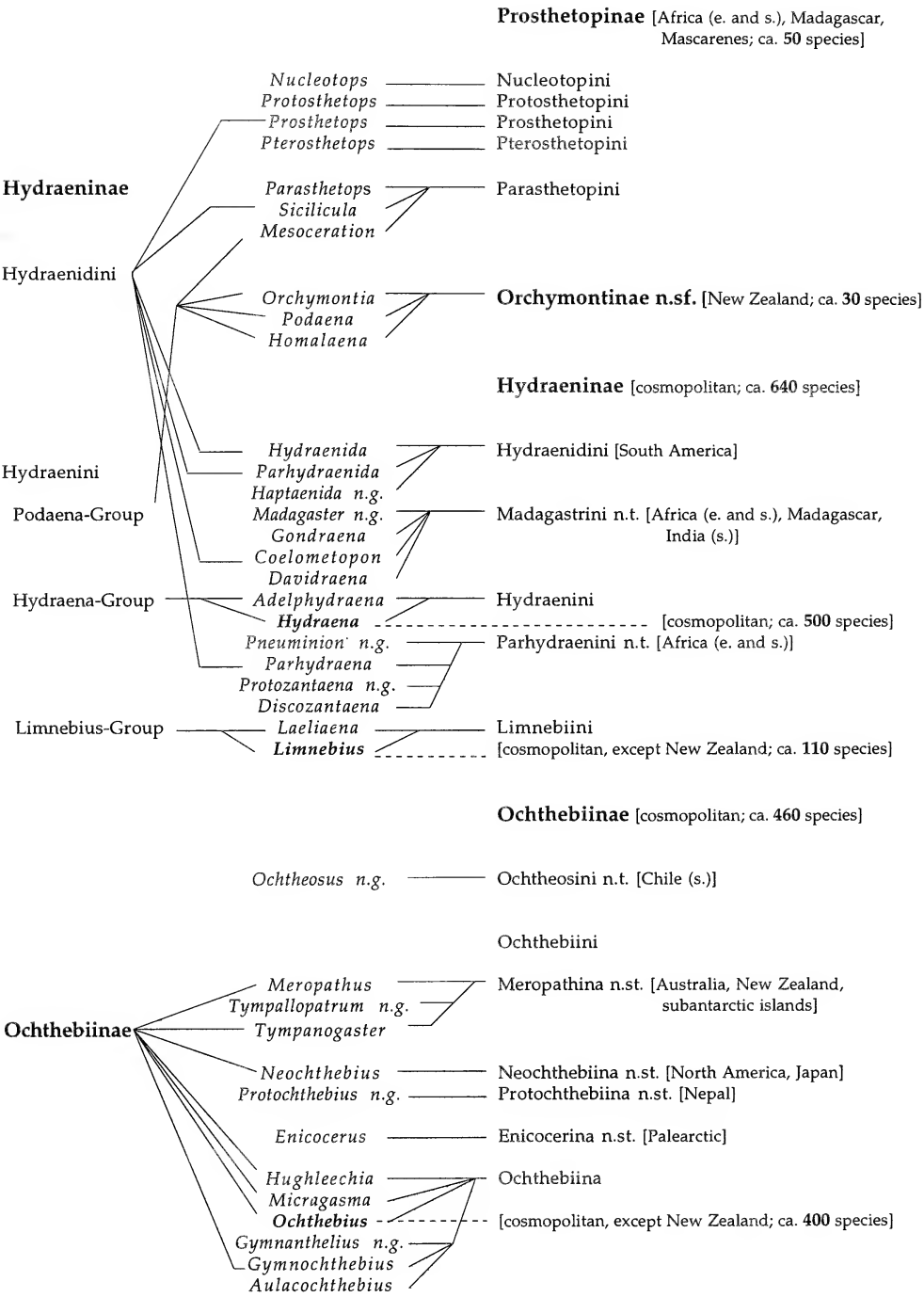
The antennal pocket of hydraenids, formed by adjacent areas of the head and prothorax, provides a rich array of new characters that are pivotal to our understanding of morphological change and phylogenetic relationships within the family. The complexity and integration of the parts of the antennal pocket are seen in their greatest expression in the specialized ESDS of *Ochthebius*, *Hydraena*,

→

Fig. 71.—Relationships and classification of the Hydraenidae as given by Hansen (1991) and as proposed herein. Putative synapomorphic and plesiomorphic characters of groups are discussed in the text and summarized in the key to taxa. Numbers of described species are approximate. The genera *Ochthebius*, *Hydraena*, and *Limnebius* comprise about 85% of described species.

Hansen, 1991

Perkins, present



and *Limnebius*, genera that have evolved secretion-grooming behavior. The relative success of these three genera, by far the most speciose (comprising nearly 85% of described species) and the most widely distributed in the family (Fig. 71), is surely related to their ability to maintain effective respiratory bubbles.

Knowledge of the ESDS provides new perspectives on the utilization of aquatic microhabitats by hydraenids. Streams and ponds are nearly worldwide, forming networks of microhabitats across a widely variable matrix of climatic, edaphic, and biotic conditions. Among hydraenids, the genera with specialized ESDS have been overwhelmingly successful in these stream and pond microhabitats. The proposition that the ESDS is pivotal to opening these widespread microhabitats to hydraenids is strengthened by the three-fold independent evolution of specialized ESDS.

However, although the genera *Ochthebius*, *Hydraena*, and *Limnebius* are common in sandy-gravelly stream margin and pond margin microhabitats, only very occasionally is a specimen of these genera found in hygropetric microhabitats, such as rock face seeps or margins of waterfalls, and members of the three genera are never benthic. This suggests that the specialized ESDS is not readily modified, via either amplification or reduction, to allow utilization of the hygropetric and benthic microhabitats. Certainly many aspects of hydraenid biology are involved in this microhabitat restriction, but one obvious possibility is that secretion-grooming behavior, which occurs out of the water, is an effective deterrent to life on vertical, wet rock faces or stream bottoms.

Contrastingly, benthic microhabitats are utilized by members of the Prosthetopinae and Orchymontinae, hydraenids that have virtually no antennal pocket. Instead of a bubble, benthic species have a thin layer of air held by plastron vestiture, eliminating the need to return to the surface for air. Reflecting the loss of the respiratory bubble-replenishing function, the antennae of these forms are in various stages of reduction and fusion, occurring independently in several lineages (Perkins and Balfour-Browne, 1994). Significantly, the antennae of some members of both the Prosthetopinae and Orchymontinae retain the condition of 11 articles, the plesiomorphic number for the family. These plesiomorphic antennae are obviously not derived from the antennae of forms with specialized ESDS, which have the preclub articles reduced in number and shaped to conform to the antennal pocket. Accepting the commonly held premise that loss of antennal articles by fusion and reduction is unidirectional, then it necessarily follows that the Prosthetopinae and Orchymontinae are not derived from any clades with specialized ESDS, all of which have loss of preclub antennal articles. The absence of an antennal pocket therefore does not represent secondary reduction from the well-formed and complex antennal pocket of ESDS lineages.

Similar antennal evidence is available for humicolous and hygropetric forms. The only Ochthebiinae retaining the ancestral, 11-articled antenna is *Ochtheosus*, a fungicolous species with primitive mouthparts and primitive internal head structure. In the Hydraeninae, seven of the 12 genera have 11-articled antennae; three of these genera are definitely hygropetric (*Parhydraenida*, *Coelometopon*, and *Madagaster*), one possibly hygropetric (*Hydraenida*), and one is humicolous (*Davidraena*). Genera with 11-articled antennae are not derived from lineages with the reduced antenna characteristic of genera with specialized ESDS.

The secondary loss of structures is always a possibility that should be addressed. For example, it is possible that the lack of ESDS structures in *Neochthebius* (Fig. 46, 47) is the result of secondary loss due to the unusual microhabitat

(cracks in intertidal rocks). However, such a reversal would require the loss without a trace of a complete character system, not just the reduction of one or two components. Some evidence, for example the retention of the periocular exocrine pores of *Meropathus*, which has reduced eyes (Fig. 41B:e), indicates that at least some exocrine-related structures are not readily lost, despite reduction of surrounding body areas. Postulating secondary losses on the absence of clear supporting evidence would be premature; such losses (if any have occurred) must be uncovered by new findings.

There are strong correlations in the body forms of hydraenids and the various specialized ESDS. I have wondered why members of *Hydraena* are so "loosely jointed" compared with other hydraenids. The ESDS explanation is that the extensive intersegmental membranes make it possible for the tibiae to effectively clean the hypomeron during secretion-grooming, by allowing extending and twisting of the prothorax. *Limnebius* has an unusual shape, being the only hydraenid having the prothorax posteriorly wide and concave, with the distal end of the middle femur fitting into the concavity; this form correlates exactly with the location of the ESDS glandular fovea and secretion-grooming behavior. The characteristic hyaline borders of *Ochthebius* is another example of the relationship of specialized body form and the ESDS.

This paper is only the beginning of our understanding of the ESDS and the antennal pocket, and the relationships of these features to the natural history and phylogeny of the family. Observations of secretion-grooming behavior and bubble formation are needed for more species of *Ochthebius*, *Hydraena*, and *Limnebius*. Grooming behavior of the remainder of the family is entirely unstudied, and certainly more new genera remain to be discovered and described. A more comprehensive view of the phylogeny of hydraenids will require these studies, in addition to a detailed morphological study of the larval forms in the family.

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APPENDIX 1

Taxa Studied in Transparency Mounts, and New Combinations(!)

Orchymontinae

Homalaena dispersa Ordish (New Zealand), *Orchymontia ciliata* Ordish (New Zealand), *O. spinipennis* Broun (New Zealand), *Podaena dentipalpis* Ordish (New Zealand).

Prosthetopinae

Mesoceration abstrictum Perkins and B.-Browne (South Africa), *M. apicalum* Perkins and B.-Browne (South Africa), *M. brevigranum* Perkins and B.-Browne (South Africa), *M. dissonum* Perkins and B.-Browne (South Africa), *M. distinctum* Perkins and B.-Browne (South Africa), *M. endroedyi* Perkins and B.-Browne (South Africa), *M. fusciceps* Perkins and B.-Browne (South Africa), *M. jucundum* Perkins and B.-Browne (South Africa), *M. languidum* Perkins and B.-Browne (South Africa), *M. rivulare* Perkins and B.-Browne (South Africa), *M. rubidum* Perkins and B.-Browne (South Africa), *M. rufescens* Perkins and B.-Browne (South Africa), *M. splendorum* Perkins and B.-Browne (South Africa), *M. sulcatulum* Perkins and B.-Browne (South Africa), *M. transvaalense* Janssens (South Africa), *M. truncatum* Perkins and B.-Browne (South Africa).

Nucleotops nimbiceps Perkins and B.-Browne (South Africa), *Parasthetops aeneus* Perkins and B.-Browne (South Africa), *P. camurus* Perkins and B.-Browne (South Africa), *P. curidius* Perkins and B.-Browne (South Africa), *P. nigritus* Perkins and B.-Browne (South Africa), *P. reflexus* Perkins and B.-Browne (South Africa), *P. rufulus* Perkins and B.-Browne (South Africa), *P. spinipes* Perkins and B.-Browne (South Africa), *Prosthetops grandiceps* Perkins and B.-Browne (South Africa), *P. megacephalus* (Boheman) (South Africa), *P. nitens* (Péringuey) (South Africa), *P. setosus* Perkins and B.-Browne (South Africa), *Protosthetops kenyensis* (Orchymont) (Kenya), *Pterosthetops equestrius* Perkins and B.-Browne (South Africa), *P. harrisoni* Perkins and B.-Browne (South Africa), *P. impressus* Perkins and B.-Browne (South Africa), *Sicilicula borbonica* J. Balfour-Browne (Reunion).

Hydraeninae

Adelphydraena orchymonti Perkins (Venezuela), *Coelometopon madidum* Janssens (Tanzania), *Coelometopon* (two n. spp., South Africa), *Davidraena bacata* n. gen., n. sp. (India), *Discozantaena genuvela* Perkins and B.-Browne (South Africa), *Hydraena (Haenydra) gracilis* Germar (France), *Hydraena (Hadrenya) minutissima* Stephens (!) (Germany), *H. (Hadrenya) pygmaea* Waterhouse (!) (Germany), *H. (Hadrenya) sharpi* Rey (!) (Spain), *Hydraena (Phothydraena) testacea* Curtis (United Kingdom, Spain).

Hydraena (sensu stricto) *accurata* Orchymont (South Africa), *H.* (sensu stricto) *americana* Jäch (U.S.A.), *H.* (sensu stricto) *angulosa* Mulsant (France), *H.* (sensu stricto) *anisonycha* Perkins (Colombia), *H.* (sensu stricto) *brevis* (Sharp) (!) (Mexico), *H.* (sensu stricto) *circulata* Perkins (U.S.A.), *H.* (sensu stricto) *cuspidicollis* Perkins (Mexico), *H.* (sensu stricto) *exarata* Kiesenwetter (Spain), *H.* (sensu stricto) *finita* Orchymont (Greece), *H.* (sensu stricto) *occidentalis* Perkins (U.S.A.), *H.* (sensu stricto) *pulchella* Germar (Slovenia), *H.* (sensu stricto) *riparia* Kugelann (France), *H.* (sensu stricto) *tussineri* Kuwert (Spain), *H.* (sensu stricto) (15 n. spp., Australia, Papua New Guinea, South Africa).

Hydraenida ocellata Germain (Chile), *H. robusta* Perkins (Chile), *Laeliaena* (n. sp., Nepal), *Limnebius hispanicus* Orchymont (Spain), *L. piceus* (Horn) (U.S.A.), *L. sinuatus* Sharp (Guatemala), *L. truncatellus* Thomson (Portugal), *Limnebius* (five n. spp., Australia, South Africa).

Madagaster steineri n. gen., n. sp. (Madagascar), *Parhydraena brevipalpis* (Régimbart) (Ethiopia), *P. jeanneli* (Orchymont) (!) (Kenya), *P. seriata* J. B.-Browne (South Africa), *Parhydraena* (five n. spp., South Africa), *Parhydraenida bubrunipes* Perkins (Brazil), *Pneuminion velamen* n. gen., n. sp. (South Africa), *Protozantaena labrata* n. gen., n. sp. (South Africa).

Ochthebiinae

Enicocerus benefossus (LeConte) (!) (U.S.A.), *E. exsculptus* (Germar) (!) (France), *Gymnanthelius clypeatus* (Deane) (!) (Australia), *G. hieroglyphicus* (Deane) (!) (Australia), *Gymnochthebius brisbanensis* (Blackburn) (!) (Australia), *G. fossatus* (LeConte) (Mexico), *G. germaini* (Zaitzev) (Chile), *G. laevipennis* (LeConte) (U.S.A.), *G. lividus* (Deane) (!) (Australia), *G. maurenae* Perkins (U.S.A.), *G. notalis* (Deane) (!) (Australia), *G. octonarius* Perkins (Argentina), *G. oppositus* Perkins (U.S.A.), *G. perlabidus* Perkins (Costa Rica), *G. plesiotypus* Perkins (Argentina), *Gymnochthebius* (four n. spp., Australia, New Guinea).

Hughleechia giulianii Perkins (Australia), *Meropathus campbellensis* Brookes (Campbell Island), *M. vectis* Perkins (Argentina), *Micragasma paradoxum* J. Sahlberg (Greece), *Neochthebius vandykei* (Knisch) (U.S.A.).

Ochthebius (Asiobates) andronius Orchymont (South Africa), *O. (A.) angularidus* Perkins (U.S.A.), *O. (A.) apache* Perkins (U.S.A.), *O. (A.) bicolor* Germar (United Kingdom), *O. (A.) brevipennis* Perkins (U.S.A.), *O. (A.) cribricollis* LeConte (U.S.A.), *O. (A.) discretus* LeConte (U.S.A.), *O. (A.) leechi* Wood and Perkins (U.S.A.), *O. (A.) martini* Fall (U.S.A.), *O. (A.) puncticollis* LeConte (U.S.A.), *O. (A.) similis* Sharp (U.S.A.).

Ochthebius (sensu stricto) *adriaticus* Reitter (!) (Greece), *O.* (sensu stricto) *arenicolus* Perkins (U.S.A.), *O.* (sensu stricto) *aztecus* Sharp (Mexico), *O.* (sensu stricto) *batesoni* Blair (Ecuador), *O.* (sensu stricto) *borealis* Perkins (U.S.A.), *O.* (sensu stricto) *capicola* (Péringuey) (South Africa), *O.* (sensu stricto) *causicus* Kuwert (India), *O.* (sensu stricto) *celatus* Jäch (!) (Malta), *O.* (sensu stricto) *difficilis* Muls. (Spain), *O.* (sensu stricto) *eburneus* J. Sahlberg (!) (Tunisia), *O.* (sensu stricto) *extremus* (Péringuey) (South Africa), *O.* (sensu stricto) *glaber* Montes and Soler (Spain), *O.* (sensu stricto) *interruptus* LeConte (U.S.A.), *O.* (sensu stricto) *lejolisi* Mulsant and Rey (!) (France), *O.* (sensu stricto) *lineatus* LeConte (U.S.A.), *O.* (sensu stricto) *marinus* (Paykull) (U.S.A.), *O.* (sensu stricto) *namibiensis* Perkins and B.-Browne (Namibia), *O.* (sensu stricto) *notabilis* Rosenhauer (Spain), *O.* (sensu stricto) *obscurus* Sharp (U.S.A.), *O.* (sensu stricto) *pagotrichus* Perkins and B.-Browne (Namibia), *O.* (sensu stricto) *pedalis* J. B.-Browne (South Africa), *O.* (sensu stricto) *pedicularius* Kuw. (Spain), *O.* (sensu stricto) *punctatus* Stephens (Spain), *O.* (sensu stricto) *quadricollis* Mulsant (!) (Madeira, Sardinia), *O.* (sensu stricto) *quadrioveolatus* Wol. (Spain), *O.* (sensu stricto) *reticulatus* Perkins (U.S.A.), *O.* (sensu stricto) *rectus* LeConte (U.S.A.), *O.* (sensu stricto) *rubripes* Boheman (!) (Namibia), *O.* (sensu stricto) *salinarius* J. B.-Browne (South Africa), *O.* (sensu stricto) *salinator* Peyerimhoff (Egypt), *O.* (sensu stricto) *serratus* Rosenhauer (!) (Morocco), *O.* (sensu stricto) *spatulus* J. B.-Browne (South Africa), *O.* (sensu stricto) *spinatus* Perkins and B.-Browne (South Africa), *O.* (sensu stricto) *subinteger* Mulsant and Rey (!) (Morocco), *O.* (sensu stricto) *uniformis* Perkins (U.S.A.), *O.* (sensu stricto) *zugmayeri* Knisch (Iran).

Ochtheosus fungicolus n. gen., n. sp. (Chile), *Protochthebius jagthanae* (Champion) (!) (Nepal), *P. satôï*, n. gen., n. sp. (Nepal), *Tympalopatrum longitutum* n. gen., n. sp. (Australia), *Tympanogaster*

cornutus (Janssens) (!) (Australia), *T. deanei* Perkins (Australia), *T. macrognathus* (Lea) (!) (Tasmania), *Tympanogaster* (three n. spp., Australia).

APPENDIX 2

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NOTEWORTHY RECORDS OF SMALL MAMMALS FROM
GHANA WITH SPECIAL EMPHASIS ON THE ACCRA PLAINSJAN DECHER¹DUANE A. SCHLITTER
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ABSTRACT

In this paper we describe new or additional records of four species of shrews (Soricidae), nine species of bats (Hipposideridae, Vespertilionidae, Molossidae), and one species of rodent (Muridae) from Ghana. These records add to our knowledge of the distribution of small mammals in Ghana especially those occurring on the Accra Plains. A zoogeographic explanation for these distributional data is sought in the context of the Dahomey Gap phenomenon.

INTRODUCTION

Little information has been published during the last three decades on the distribution and systematics of Ghanaian mammals. The most recent effort of documenting populations of terrestrial mammals in southern Ghana was that by Yeboah (1984), who studied the ecology of small rodents in primary forest and farmland at Kukurantumi near Koforidua, southeastern Ghana, and was the first to report *Steatomys cuppedius* from an area south of the Guinea savanna. To date, our knowledge of Ghanaian shrews, bats, rodents, and small carnivores is patchy, if not anecdotal, throughout much of the region. A comprehensive review of the mammals of Ghana is badly needed.

This paper reports new records of small mammals from Ghana. These records augment those previously mentioned in checklists of Ghanaian mammals (Ingoldby, 1929; Cansdale, 1948; Booth, 1956, 1959) and the relevant chapters in Mammal Species of the World (Wilson and Reeder, 1993) or considerably extend the known range for these species in Ghana. Additional species are added to the list of forest and savanna mammals peculiar to the Dahomey Gap, the conspicuous interruption of the West African high forest belt in the region of southeastern Ghana, Togo, and Benin. Jeník (1984, 1994) interpreted the Dahomey Gap phenomenon as a result of cooler offshore upwellings near Cape Palmas, Liberia, and Cape Three Points, Ghana. On the Accra Plains, this coastal upwelling leads to abnormally arid climate with characteristic dry forest or savanna vegetation types (Jeník and Hall, 1976). The Accra Plains have also been termed the "core area" of the Dahomey Gap (Jeník, 1994:130) with a mean annual rainfall from just 733

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mm (Accra) to 1117 mm (Akuse). The mixture of savanna and forest mammalian faunal elements in the Dahomey Gap was first discussed by Booth (1954, 1958, 1959) and later reevaluated by Robbins (1978).

MATERIALS AND METHODS

Specimens were collected between October 1991 and June 1992 as part of a study of small mammal ecology on the Accra Plains of Ghana (Fig. 1; Appendix). Most terrestrial mammals were collected on 1-ha trapping grids with 100 stations each supplied with two Sherman live traps. In addition, Museum Special snap traps were used during a field trip to the area of Yendi and Bimbila, northeastern Ghana, in November 1991. Bats were collected with mist nets. The *Otomops* specimen collected in 1968 and catalogued at the United States National Museum of Natural History (USNM), Washington, D.C., (USNM 420099) was included because until recently this bat was known only from East and South Africa (Long, 1995). All other specimens, including frozen tissues for future examination, are housed at the Carnegie Museum of Natural History (CM), Section of Mammals, Pittsburgh, Pennsylvania, and the J. F. Bell Museum of Natural History at the University of Minnesota (MMNH), Saint Paul, Minnesota. A synoptic collection was returned to the Ghana Department of Game and Wildlife, Accra.

External measurements were recorded in the field to the nearest millimeter. Cranial measurements were obtained with digital calipers to the nearest 0.1 mm. Mensural variates for the shrews were: total length; head, body and tail; tail; hindfoot; ear; mass (g); condylo-incisive length of the skull; least intraorbital width; greatest maxillary breadth; greatest width of braincase; greatest height of braincase; and greatest length of upper tooth row, following Hutterer and Happold (1983). In addition, for bats we used: forearm, condylo-canine length, width across last molar, and length of maxillary tooth row (C-M³), following Qumsiyeh (1985) and Koopman (1975); and for rodents: upper cheekteeth row, and zygomatic breadth following Van der Straeten and Verheyen (1978). Nomenclature follows Wilson and Reeder (1993), unless otherwise noted.

TAXONOMIC ACCOUNTS

Insectivora

Family Soricidae

Crocidura buettikoferi Jentink, 1888

This is a medium shrew with dark brown dorsal fur and slightly paler grayish-brown ventral pelage. The tail is covered with very short hairs and a few scattered bristles. Only one female was collected on 12 February 1992 at Adumanya Sacred Grove—a traditionally protected 1.5-ha remnant of high forest, near Dodowa, at the foot of the Akwapim escarpment on the northwestern Accra Plains (Fig. 1; Table 1). This grove is surrounded by farmland. The female was pregnant with a single embryo each in the left and right uterine horns.

Hutterer and Happold (1983:49) stated that, in Nigeria, "According to collectors' notes, *C. buettikoferi* lives in grassland habitats in the rainforest zone rather than in forest habitats." However, we collected our specimen in a high forest habitat. This species has not been reported previously from Ghana (Hutterer, 1993), and attempts to collect it in the Ivory Coast failed (Heim de Balsac, 1968), even though its type specimen is from Robertsport, Liberia (Jentink, 1888).

Crocidura crossei Thomas, 1895

This is a pale, grayish shrew with a light gray ventral pelage contrasting with darker dorsal fur. The tail bristles are more dense than in *C. buettikoferi*. Four

→

Fig. 1.—Map of the Accra Plains and Ghana (insert) showing collecting localities mentioned in the text.

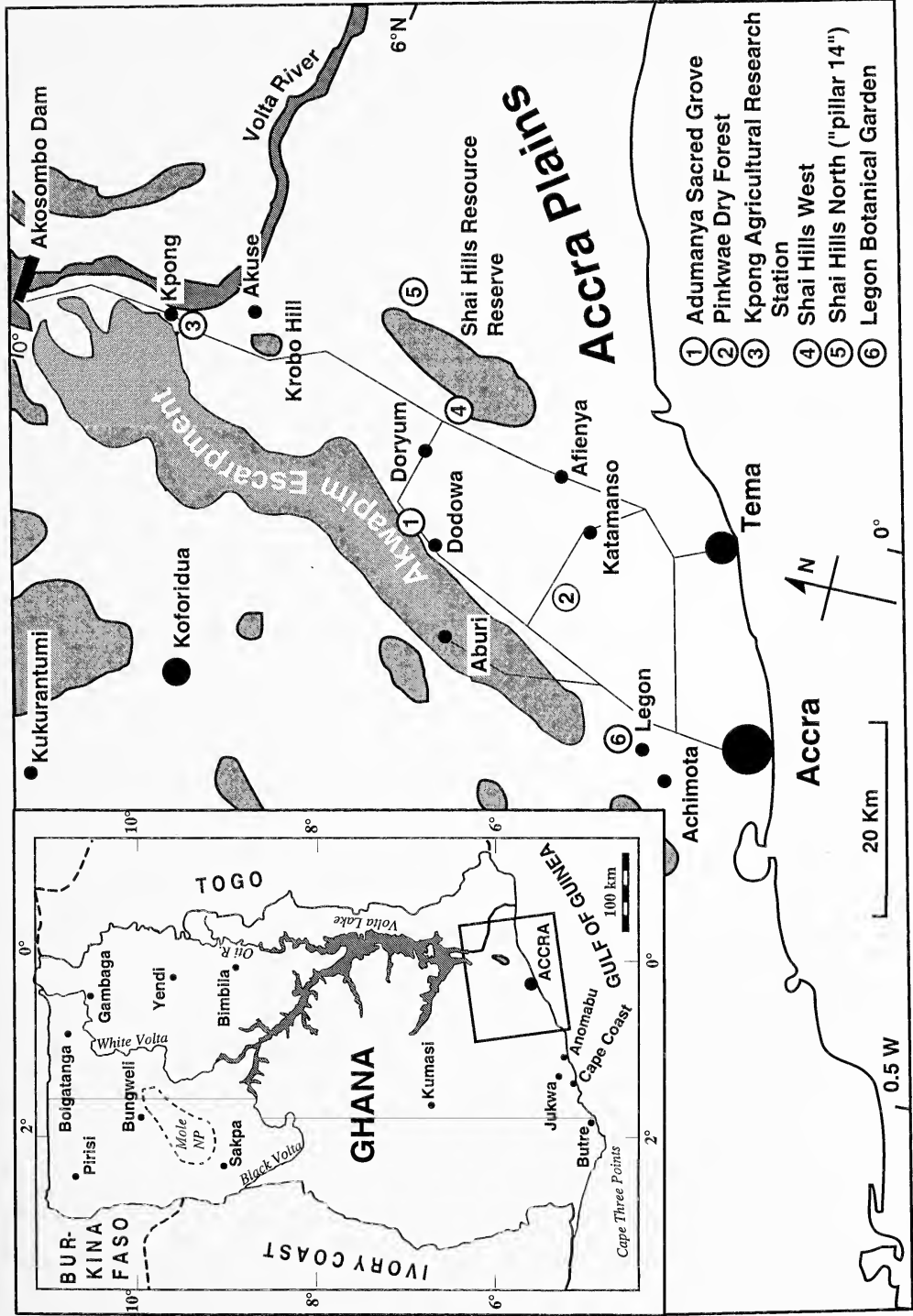


Table 1.—Selected external and cranial measurements (mm; $\bar{x} \pm SD$ [range]) of *Crocidura buettikoferi* and *C. crossei*. Sample sizes are given in parentheses in column headings. Raw measurements are given for samples of 1–2 specimens; summary statistics are limited to ranges for the sample of *C. buettikoferi* from Nigeria.

Variate	<i>Crocidura buettikoferi</i>				<i>Crocidura crossei</i>		
	Nigeria		Ghana		Ghana		Nigeria
	Females (1) ^a	Females (3) ^b	Umuahia		Females (4) ^c	Males (5) ^d	Both sexes (10) ^e
Total length	142	—			117.0 \pm 1.83 (115–119)	116.6 \pm 3.44 (114–122)	—
Tail length	52	51–62			47.8 \pm 2.22 (45–50)	48 \pm 3.24 (45–51)	48–57
Hindfoot length	14	12–15			12.3 \pm 0.5 (12.0–13.0)	12.2 \pm 1.09 (11.0–13.0)	10–12
Ear length	13	7.0–9.5			9.8 \pm 1.5 (8.0–11)	9.8 \pm 1.3 (8.0–11.0)	6–8
Mass (g)	10	—			5.1 \pm 0.75 (4.5–6.0)	5.6 \pm 0.89 (5.0–7.0)	6.3–8.0
Condylar-incisive length	21.9	21.4–22.7			18.8 \pm 0.79 (18.1–19.6)	18.7 \pm 0.58 (17.9–19.4)	18.5–19.9
Intraorbital width	4.5	4.9–5.1			3.6 \pm 0.13 (3.4–3.7)	3.7 \pm 0.08 (3.6–3.8)	4.0–4.4
Greatest maxillary breadth	7.2	6.7–7.1			5.7 \pm 0.32 (5.3–5.9)	5.7 \pm 0.18 (5.5–5.9)	5.5–6.0
Width of skull	9.8	9.2–9.9			7.8 \pm 0.26 (7.5–8.1)	8.0 \pm 0.21 (7.7–8.2)	7.8–8.5
Height of braincase	5.4	5.2–5.8			4.1 \pm 0.19 (3.9–4.3)	4.3 \pm 0.31 (3.9–4.6)	4.4–4.7
Upper tooth row	9.8	10.0–10.1			8.1 \pm 0.28 (7.9–8.5)	8.0 \pm 0.27 (7.7–8.3)	7.7–8.6

^a Specimen CM 113501.

^b After Hutterer and Happold (1983).

^c Specimens CM 113503, 113505, 113507, and 113508.

^d Specimens CM 113502, 113504, 113506, 113509, and 113510.

females and four males of this shrew were captured during the dry season, between 3–5 December 1991, at Pinkwae Dry Forest, another 120-ha sacred grove on the Accra Plains. A single male was caught in a *Gmelina* forest plantation near the University of Ghana Agricultural Research Station at Kpong (Fig. 1; Table 1). Both are relatively undisturbed forests surrounded by savanna and farmland. Only one of the four females captured at Pinkwae was pregnant with two embryos, one in each uterine horn.

In western Nigeria this species occurred throughout the “rainforest zone, and relic forests in derived savanna . . .” (Hutterer and Happold, 1983:62). The occurrence in a sacred grove and a tree plantation on the Accra Plains may point to a less specialized distribution requiring closed canopy forests of a variety of types including the unique dry “south-east outlier type” of the Accra Plains (Hall and Swaine, 1981:87).

Crocidura lamottei Heim de Balsac, 1968

This is a medium-sized shrew with lighter colored pelage. The gray venter is washed with a yellowish tint and contrasts with the gray-brown dorsal fur. The tail has densely arranged short bristles. The hindfoot is very short. The vibrissae are long and the ears small. Two females were caught at Pinkwae Dry Forest on the Accra Plains on 17 and 26 November 1991, during the beginning of the dry season (Table 2). The latter one was pregnant with one embryo in the left uterine horn.

In size these specimens are slightly larger than specimens from Guinea, Ivory Coast, and Togo reported by Heim de Balsac (1968) in his description of the species. They agree more closely with three individuals reported by Hutterer and Happold (1983) from southwestern Nigeria, and with the specimens from Senegal, Burkina Faso, and northern Nigeria which Hutterer (1986) included in the subspecies *C. lamottei elegans*. The species is now known from a variety of habitats, including rainforest (Korup National Park; Hutterer and Schlitter, 1996), clearings in the forest zone (Owerri, Nigeria; Hutterer, 1986), Guinea savanna (Mt. Nimba, Guinea, and Ivory Coast; Heim de Balsac, 1968), and Sudan savanna (Bandia, Senegal; Hutterer, 1986).

The new specimens constitute the second record of Lamotte’s shrew from southern Ghana. Hutterer (1986) recorded it from Achimota, Accra Plains. His manuscript listed two other localities from Ghana, Legon and Pinkwae, but these were lost apparently during the publishing process. Skulls extracted from owl pellets from these three localities are deposited in the collections of the Museum Alexander Koenig, Bonn, Germany. Other specimens from Ghana were from Kokofu, Brong Ahafo Region (USNM 424636), and Pulima, Upper West Region (USNM 414681). According to present knowledge the range of *C. lamottei* extends across most of the savannas of West Africa but nowhere as close to the coast as on the Accra Plains.

Crocidura nigeriae Dollman, 1915

Crocidura nigeriae is not quite as dark brown as *C. buettikoferi*, with a few distinct long bristles on the tail. The dorsal fur has a slightly grizzled appearance. This species was caught only at Yendi and Bimbila in the Northern Region of northeastern Ghana (Table 2). These specimens are the first records of this species west of Nigeria.

Table 2.—Selected external and cranial measurements (mm; $\bar{x} \pm SD$ [range]) of *Crocidura lamottei* and *C. nigeriae*. Sample sizes are given in parentheses in column headings. Raw measurements are given for samples of 1–2 specimens; summary statistics are limited to ranges for the sample of *C. nigeriae* from Ghana.

Variate	<i>Crocidura lamottei</i>				<i>Crocidura nigeriae</i>			
	Ghana		SW Nigeria		Guinea, Ivory Coast, Togo		Ghana	
	Females (2) ^a		Males (2), females (1) ^b		Both sexes (5–9) ^c		Males (3) ^d	
							Males (3) ^e	
Total length	138, 140		—		—		159 \pm 13.5 (144–170)	—
Tail length	51, 46		52–55		35.5–52.0 (5)		56.7 \pm 4.0 (53–61)	67
Hindfoot length	14, 14		15–16		14.0–15.5 (5)		17 \pm 1 (16–18)	15.5
Ear length	10, 12		11–12		—		11.3 \pm 2.5 (9–14)	9.5
Mass (g)	17.5, 11.0		18–23		—		20.3 \pm 4.7 (15–24)	6.3–8.0
Condylar-incisive length	26.8, 25.2		24.7–25.8		25.5–26.0 (7)		25.8 \pm 1.2 (24.4–26.6)	25.9
Intraorbital width	4.9, 4.8		4.7–5.4		4.7–5.0 (8)		4.9 \pm 0.2 (4.7–5.0)	5.1
Maxillary breadth	8.2, 8.4		8.1–8.8		7.8–8.5 (8)		8.1 \pm 0.4 (7.6–8.3)	7.8
Width of skull	10.7, 10.5		10.1–10.6		—		10.7 \pm 0.5 (10.3–11.3)	10.5
Height of brain case	5.9, 5.7		5.7–6.2		5.7–6.0 (7)		6.1 \pm 0.2 (5.9–6.2)	6.8
Upper tooth row	11.9, 11.4		11.1–11.5		10.4–11.8 (9)		11.6 \pm 0.4 (11.2–12.0)	11.5

^a Specimens CM 113511, 113512.

^b After Hutterer and Happold (1983).

^c After Heim de Balsac (1968).

^d Specimens CM 113516, 113517, 113518, 113519.

^e Specimens CM 113513, 113514, 113515.

^f After Dollman (1915).

Table 3.—Selected external and cranial measurements (mm; $\bar{x} \pm SD$ [range]) for *Hipposideros abae*. Sample sizes are given in parentheses in column headings. Raw measurements are given for samples of 1–2 specimens; summary statistics are limited to ranges for the sample of female *H. abae* from Anamabu, Ghana.

Variate	Ghana			Burkina Faso	Cameroon
	Pinkwae Forest	Anamabu		Diebougou	Karba Manga
	Females (2) ^a	Females (3) ^b	Males (2) ^c	Males (2) ^d	Males (1) ^e
Total length	105, 99	—	—	—	—
Tail length	30, 34	35 \pm 4.36 (30–38)	35, 34	35, 31	31
Hindfoot length	13, 13	11 \pm 0.0 (11)	10.5, 10.0	6.5, 9.0	10
Ear length	21, 22	21.3 \pm 1.15 (20–22)	18.5, 19.0	22, 21	20
Mass (g)	25.5, 20.0	—	—	—	—
Forearm length	59.7, 60.0	59.67 \pm 1.15 (59–61)	61, 60	57.0, 55.5	58
Condylar-canine length	19.2, 19.1	—	—	—	20
Width across molars	8.9, 9.0	—	—	8.85, 8.50	9.1
C–M ³	8.7, 8.8	9.17 \pm 0.29 (9.0–9.5)	9, 9	8.9, 9.0	8.9

^aSpecimens CM 113596, 113597.

^bAfter Hayman (1945); specimens BM 46.108, 46.109, 46.233.

^cAfter Hayman (1945); specimens BM 46.107, 46.232.

^dAfter Koch-Weser (1984); SMF 60987, 60988.

^eAfter Aellen (1952); no. 1261.

Hutterer and Happold (1983:51) report this species as “widespread in rainforest zone and parts of derived savanna,” while we found it only in the northern Guinea savanna in Ghana. Previously regarded as a subspecies of *C. poensis* (Heim de Balsac and Meester, 1977), this shrew was subsequently recognized as a separate species on the basis of its different karyotype— $2n = 50$, $FN = 76$ versus $2n = 52$, $FN = 70$ in *C. poensis* (Meylan and Vogel, 1982).

Chiroptera
Family Hipposideridae
Hipposideros abae J. A. Allen, 1917

Two females were caught at Pinkwae Forest, Accra Plains, on 10 and 15 April 1992. Both are of the bright orange color phase mentioned by Rosevear (1965) and Happold (1987). This species has not been reported from the Accra Plains before, but Hayman (1945) gives measurements for two males and three females from Anamabu, Cape Coast, Ghana, housed at the Natural History Museum, London (BMNH). These and a female with the locality “Anomabu,” Central Region, Ghana, at the Field Museum of Natural History (FMNH), Chicago, Illinois (FMNH 54495), were collected by G. S. Cansdale in 1945. There is also one male at the USNM (USNM 414239), collected by J. C. Geest at Butre in the Western Region, and another male specimen from Mole National Park, “near Bungweli” in the Northern Region of Ghana (cf. Fig. 1), at the American Museum of Natural History (AMNH), New York (AMNH 237421). In a comparison of measurements (Table 3), the Accra Plains specimens agree well with those published from Anamabu (Hayman, 1945), two Burkina Faso specimens (Koch-Weser, 1984), and one Cameroon specimen (Aellen, 1952). In Burkina Faso, *H. abae* was found roosting in association with *H. caffer*, *H. jonesi*, *Rhinolophus landeri*,

and *Lissonycteris angolensis* in a subterranean bunker (Koch-Weser, 1984). In his checklist of Gold Coast mammals, Cansdale (1948) notes that *H. abae* was found together with *H. caffer guineensis* inside Anamabu Castle. This bat is relatively rare and has a wide distribution from Guinea Bissau to Uganda (Hill, 1963; Rosevear, 1965).

Family Vespertilionidae
Eptesicus guineensis (Bocage, 1889)

Rosevear (1965) pointed to the deep chestnut-brown color as one characteristic of this dark-winged *Eptesicus*. Two males and four females were caught. Two of the females, taken on 2 November 1991 at Bimbila in the Northern Region, were lactating. All the others were caught on the Accra Plains. One male was netted at the University of Ghana, Legon, Botanical Garden, on 14 November 1991; a male and female were captured at a waterhole in the northeastern Shai Hills Resource Reserve on 13 January and 6 May 1992, respectively; and on 19 May 1992, one individual was caught at the southwestern end of the Shai Hills Resource Reserve (Fig. 1; Table 4). Koch-Weser (1984) pointed out the sexual dimorphism (females are larger) in this species.

This bat occurs from Senegal to Ethiopia and northeastern Zaire. It was reported from several localities in Burkina Faso (Koopman et al., 1978; Koch-Weser, 1984) and seems to occur throughout the savanna zones of Ghana. There is one additional specimen from Subinja, 2 mi E Wenchi, Brong Ahafo Region, at the USNM (USNM 414983). It appears that this bat inhabits the various savanna types of West Africa, reaching the coast where vegetation and climate permit, as on the Accra Plains, or at Conakry, Guinea (Rosevear, 1965).

Eptesicus capensis (A. Smith, 1829)

All four individuals of this species were captured at two waterholes in the northeast and northwest portions of the Shai Hills Resource Reserve on the Accra Plains. Two females and one male were caught on 12 November 1991 and one female with two embryos was netted on 13 January 1992. Measurements (Table 4) are compared to those from Sudan (Rosevear, 1965; Koopman, 1975; McLellan, 1986).

Eptesicus capensis is even more widespread in Africa than *E. guineensis*. The occurrence on the Accra Plains extends its range to the coastal savanna. Two specimens were reported from Aledjo and Niamtougou, northern Togo, by De Vree et al. (1970). These records indicate that this bat probably occurs throughout the "Dahomey Gap" region, thus confirming Rosevear (1965:257) who stated that "bats assignable to this species may therefore be expected throughout West Africa and in all zones, though possibly more commonly in the forest and Guinea woodlands, and perhaps not at all in the Sahara."

Pipistrellus aegyptius (Fischer, 1829)

A single specimen was caught at the "Pillar 14" waterhole in the Shai Hills Resource Reserve (Table 5). This is the first record of this species south of the West African Guinea Woodland. Geographically, the next closest record is a male from Nobéré, Burkina Faso (Koopman et al., 1978, as *P. deserti* Thomas, 1902). This latter specimen is housed at the Royal Ontario Museum (ROM), Toronto, Canada, and has a forearm length of only 25.9 mm (Qumsiyeh, 1985).

Table 4.—Selected external and cranial measurements (mm; $\bar{x} \pm SD$ [range]) of *Eptesicus guineensis* and *E. capensis*. Sample sizes are given in parentheses in column headings. Raw measurements are given for samples of 1–2 specimens; summary statistics are limited to ranges for specimens from Ghana.

Variate	<i>Eptesicus guineensis</i>						<i>Eptesicus capensis</i>			
	Ghana		Burkina Faso ^c		Ghana		Sudan		West African localities ^e	
	Females (4) ^a	Males (2) ^b	Females (2)	Males (1)	Females (3), males (1) ^a	Guinea ^d	(n) ^f			
Total length	77.8 \pm 2.8 (75–81)	71, 77	—	—	79.3 \pm 3.1 (75–82)	—	—	—	—	—
Tail length	29.8 \pm 5.2 (22–33)	25, 31	32.0, 33.5	30	28.8 \pm 3.95 (23–32)	25	27.5 (26–29)	(2)	28–38	—
Hindfoot length	6.4 \pm 0.8 (6.0–7.5)	7, 6	—	—	6 \pm 0 (6)	—	—	—	—	—
Ear length	9.0 \pm 1.2 (8–10)	9, 10	9.0, 10.5	9.3	9.5 \pm 1.7 (7.0–11.0)	9	11.5 (11–12)	(2)	—	—
Mass (g)	3.8 \pm 0.5 (3.0–4.0)	4, 3	—	—	4 \pm 0 (4)	—	2.5–4.0	(6)	—	—
Forearm length	28.5 \pm 0.96 (27.5–29.6)	27.9, 26.3	26.2, 29.1	26.7	28.7 \pm 0.5 (28.2–29.3)	26	28–33	(11)	29–36	—
Condylar length	11.0 \pm 0.3 (10.6–11.2)	10.7, 10.7	10.7	10.5	11.5 \pm 0.3 (11.2–11.6)	11	12.0–12.6	(4)	12.5–14.9	—
Width across molars	4.8 \pm 0.2 (4.5–5.0)	4.9, 4.7	—	—	5.3 \pm 0.0 (5.3)	—	5.2–5.7	(4)	5.2–6.3	—
C–M ³	4.0 \pm 0.2 (3.7–4.2)	3.7, 3.9	3.7	3.65	4.3 \pm 0.1 (4.2–4.4)	3.5	4.1–4.4	(4)	4.5–5.5	—

^aSpecimens CM 113618, 113619, 113621, 113622.

^bSpecimens CM 113617, 113620.

^cAfter Koch-Weser (1984).

^dAfter Rosevear (1965); type specimen.

^eSpecimens CM 113613, 113614, 113615, 113616.

^fCombined after Koopman (1975) and McLellan (1986).

^gAfter Rosevear (1965).

Table 5.—Selected external and cranial measurements (mm; $\bar{x} \pm SD$ [range]) of *Pipistrellus aegyptius* and *P. nanulus*. Sample sizes are given in parentheses. Raw measurements are given for samples of 1–2 specimens; summary statistics are limited to ranges for the sample of *P. nanulus* from Ghana.

Variate	<i>Pipistrellus aegyptius</i>					<i>Pipistrellus nanulus</i>			
	Ghana	Algeria	Libya	Ghana		West African localities ^c		East Africa ^d	
	Shai Hills	Beni Abbes	Fezzan	Ghana					
	Males (1) ^a	Females (2), males (2) ^b	Males (1) ^c	Females (3), males (1) ^d					
Total length	80	—	—	67.8 \pm 2.06 (65–69)		—		—	
Tail length	34	34–37	33	23 \pm 1.4 (21–24)		25.0–27.5		21–25	
Hindfoot length	8	6.0–7.0	6.2	6.1 \pm 1.2 (4.5–7.0)		—		—	
Ear length	10	11.0–12.5	10	9.5 \pm 1.0 (8.0–10.0)		—		—	
Mass (g)	3	—	—	4 \pm 0.4 (3.5–4.5)		—		5.0–5.5	
Forearm length	30.5	31.5–33.0	29.5	26.2 \pm 0.91 (24.9–27.0)		25.5–31.0		21–25	
Condylar-canine length	11.1	11.6–12.4	11.0	10.2 \pm 0.4 (9.9–10.8)		—		—	
Width across molars	4.9	—	—	4.7 \pm 0.1 (4.6–4.8)		5.0–5.3		—	
C–M ³	4.1	4.3–4.6	4.2	3.6 \pm 0.3 (3.1–3.8)		3.9–4.0		—	

^a Specimen CM 113631.

^b After Qumsiyeh (1985).

^c After Qumsiyeh (1985) (holotype of *P. deserti*).

^d Specimens CM 113632, 113633, 113634, and 113635.

^e After Rosevear (1965).

^f After Kingdon (1974).

Pipistrellus nanulus Thomas, 1904

All four specimens were caught in the north of Shai Hills Resource Reserve at the edge of a man-made waterhole (Table 5). Two females caught on 18 and 23 January 1992 carried two and one embryos, respectively. This species has the shortest forearm of all bats caught in the study, although slightly larger than the 21–25 mm range reported in Kingdon (1974).

This tiny bat is known from the high forest zone from Sierra Leone to Kenya and Bioko (De Vree et al., 1969; Jones, 1971; Happold, 1987; Koopman, 1993). Single specimens were reported from Mount Nimba, Liberia (Wolton et al., 1982), and from Ahoué-Ahoué, Togo (De Vree et al., 1969) but no measurements were given.

Nycticeinops schlieffeni (Peters, 1859)

Only one female with light brown dorsal fur, beige-colored ventral pelage, and a lancet-shaped tragus was caught at the waterhole in the northern Shai Hills Resource Reserve (Table 6). We follow Hill and Harrison (1987) regarding the generic name of this bat, distinguishing it from the American *Nycticeius humeralis* on the basis of the morphology of its baculum. This savanna species was previously known from the “Fra-fra Country” on the White Volta, where it was “found in huts” (de Winton, 1899:355; Rosevear, 1965) and also from Gambaga in north-eastern Ghana (Ingoldby, 1929) but it has never been reported from anywhere in southern Ghana. Specimens of *N. schlieffeni albiventer* have been reported from Paio and Fazao, Togo (De Vree et al., 1969, 1970) and several localities in Burkina Faso (Koopman et al., 1978; Koch-Weser, 1984) but all previous records in the region were from localities north of 8°N latitude in West Africa. *Nycticeinops schlieffeni* ranges widely from Mauritania eastward “to Egypt, the Sudan, Somalia, and southwestern Arabia, thence through much of eastern Africa to Mozambique, South Africa, Botswana, and Namibia” (Hill, 1983:56f). There are currently two karyotypes recognized under the name *N. schlieffenei*, $2n = 42$ and $FN = 50$ for 22 specimens from southern Africa (Rautenbach et al., 1993) and $2n = 34$ and $FN = 52$ for one specimen from Somalia (Ruedas et al., 1990).

Scotoecus albofuscus Thomas, 1890

This bat has not previously been reported from Ghana but is known in West Africa from Gambia, Senegal, Sierra Leone, Ivory Coast, and Nigeria (Hill, 1974). However, there are also specimens from Doryum on the Accra Plains in the collection of the Royal Ontario Museum (ROM), Canada (W. F. H. Ansell, personal communication). The four new specimens from Ghana were collected in the open savanna near a waterhole at the northeastern Shai Hills Resource Reserve. The female, netted on 13 January 1992, was not reproductively active (Table 6). Very little is known about the natural history of this species. Specimens from Nigeria were also caught “near a marsh” and “close to the water” (Happold, 1987:68).

Myotis bocagei (Peters, 1870)

One male of this distinctly coppery-red vespertilionid was caught at the University of Ghana Agricultural Research Station at Kpong, near the River Volta, in a mist net set at the edge of a *Gmelina* tree plantation (Table 7). Two females

Table 6.—Selected external and cranial measurements (mm; $\bar{x} \pm SD$ [range]) of *Nycticeinops schlieffeni* and *Scotoecus albofuscus*. Sample sizes are given in parentheses in column headings. Raw measurements are given for samples of 1–2 specimens; summary statistics are limited to ranges for the sample of *S. albofuscus* from Ghana.

Variate	<i>Nycticeinops schlieffeni</i>			<i>Scotoecus albofuscus</i>			
	Ghana		African localities ^a	Ghana			West Africa ^d
	Shai Hills			Shai Hills			
	Males (1) ^a			Males (3) ^d		Females (1) ^c	
Total length	79	—	—	84 ± 1.0 (83–85)	—	—	—
Tail length	33	26–35	—	27.3 ± 2.1 (25–29)	—	—	30–32
Hindfoot length	6	—	—	9 ± 0 (9)	—	—	—
Ear length	11	—	—	12.3 ± 0.6 (12–13)	—	—	—
Mass (g)	5.0	—	—	7.8 ± 1.3 (6.5–9.0)	—	6.5	—
Forearm length	29.2	30.0–33.0	—	29.0 ± 0.6 (28.5–29.7)	—	30.0	29.8–31.0 (4)
Condylar-canine length	11.7	—	—	12.5 ± 0.1 (12.4–12.6)	—	12.3	12.7–13.5 (3)
Width across last molar	5.5	5.3–5.9	—	6.4 ± 0.2 (6.2–6.6)	—	6.5	6.6–6.7 (3)
C-M ³	4.5	4.3–4.7	—	4.8 ± 0.1 (4.7–4.8)	—	4.9	4.7–5.0 (4)

^aSpecimen CM 113630.

^bAfter Rosevear (1965).

^cAfter Koch-Weser (1984).

^dSpecimens CM 113637, 113639, and 113640.

^eSpecimen CM 113632.

^fAfter Hill (1974).

Table 7.—Selected external and cranial measurements (ranges) of *Myotis bocagei*, *Glauconycteris variegata*, and *Otomops martiensseni*. Sample sizes are given in parentheses in column headings. Raw measurements are given for samples of 1–2 specimens.

Variate	<i>Myotis bocagei</i>			<i>Glauconycteris variegata</i>			<i>Otomops martiensseni</i>		
	Ghana		Ivory Coast	Ghana		West Africa ^a	Ghana		East and Central Africa
	Kpong	Males (1) ^a		West Africa	Toyebli		Shai Hills	Pirisi	
				(3) ^b	Females (4) ^c	Females (2) ^d	Males (1) ^f		
Total length	95	—	—	—	90, 106	137	—		
Tail length	42	36–42	—	—	35, 45	40	44–50 ^e		
Hindfoot length	10	—	—	8.0–8.7	8, 10	25	—		
Ear length	14	—	—	15.3–16.0	13, 15	32	—		
Mass (g)	9.5	—	—	—	7.5, 11.0	28	31.0–38.5 ^e		
Forearm length	36.8	36.5–38.5	—	35.6–37.4	41.4, 43.5	66.6	62–72 ^e		
Condylar-canine length	13.6	—	—	13.3–14.0	12.9, 13.1	—	27.0 ^g		
Width across molars	6.0	5.6–5.8	—	5.7–5.8	6.8, 6.8	—	—		
C-M ³	5.5	5.1–5.5	—	5.2–5.5	4.5, 4.7	9.8	10.8 ^g		

^a Specimen CM 113629.
^b After Rosevear (1965).
^c After De Vree (1971).
^d Specimens CM 113628 and MNH 16671.
^e After Kingdon (1974).
^f Specimen USNM 420099.
^g After Hill (1983).

taken at the Saruwi River near Jukwa in the Central Region of Ghana are housed at the USNM (USNM 412115–6) and there is a specimen from Boti Falls, Eastern Region, at the ROM, Canada (W. F. H. Ansell, personal communication). The species has also been reported previously from Borgou, Togo (De Vree and Van der Straeten, 1971); Toyebli, Ivory Coast (De Vree, 1971); and near Harbel, Liberia (Sanborn, 1949).

Glauconycteris variegata (Tomes, 1861)

Two females of this species were caught at the waterhole in the grasslands of the northern Shai Hills Resource Reserve (Table 7). This bat is easily identified by the striking dark, reticulate pattern on its pale-brown wings. Two specimens from Sakpa in the Northern Region and from Odomi Jongo in the Volta Region are housed in the USNM (USNM 420077, 424900). Specimens are also known from Mole National Park, (Hill and Harrison, 1987) and from Gambaga (Ingoldby, 1929), both localities in the Northern Region of Ghana. No other specific localities of specimens from the Accra Plains or elsewhere in Ghana have previously been published.

Family Molossidae

Otomops martiensseni (Matschie, 1897)

This is a large-sized, large-eared, colonial, and cave-dwelling molossid occurring primarily in eastern and southern Africa and Madagascar. It has been reported from the Central African Republic to Djibouti and to Angola and South Africa (Koopman, 1993; Long, 1995).

A single young adult specimen was obtained by Julius C. Geest (USNM 420099) from Pirisi (10°07'N, 2°27'W) in Guinea woodland in the Upper Region of Ghana on 1 March 1968 (Fig. 1; Table 7). In his field notes from 29 February 1968, Geest recorded that this bat was brought to him by a little girl whose "story suggests that it was hanging free in a very large fruit tree among the branches and she knocked it down with a rock. . . . Unfortunately there seems to be a fetish about the bats in the fruit tree." Attempts by him to obtain additional specimens or even visit the tree himself were unsuccessful.

Kingdon (1974:340) described these bats as "built for speed" and that they "should be capable of feeding at considerable distance from their roost." Perhaps this specimen got disoriented by several hundred kilometers from its roost. The closest known record is from Bamingui-Bangoran National Park, Central African Republic (Hill, 1983), a distance of almost 3000 km to the east. Geest's field notes suggested that if *Otomops* occurs regularly in northern Ghana it might be found inside hollow trees or cliffs. The only specimen Verschuren (1957) reported from Garamba National Park, northern Zaire, was, in fact, found in a hollow tree trunk. Few if any caves of any kind occur in the Pirisi area of northern Ghana.

Rodentia

Family Muridae

Myomys derooi Van der Straeten and Verheyen, 1978

A single female of this commensal rodent was trapped in a house in Mamobi, Accra, on 17 June 1992. A male was caught at 1 km S, 4.5 km W Yendi in the Northern Region on 17 November 1991 (Table 8). Although Van der Straeten and Verheyen (1978) reported nine localities from Ghana when they described this

Table 8.—Selected external and cranial measurements (mm; $\bar{x} \pm SD$ [range]) of *Myomys derooi*. Sample sizes are given in parentheses in headings or following ranges. Raw measurements are given for samples of 1–2 specimens.

Variate	Accra and Yendi, Ghana		Togo, Benin, and Ghana (Oda) ^b	
	Females (1), males (1) ^a		Females	Males
Total length	[185], 227		—	—
Tail	[73], 115		116.3 (98.0–135.0) (51)	114.4 (84.0–136.0) (37)
Hindfoot length	21, 20		21.3 (19.5–23.1) (64)	21.5 (19.0–23.1) (42)
Ear	17, 15		14.0 (11.7–16.8) (66)	14.7 (12.0–17.7) (43)
Mass (g)	31, 20		—	—
Condyllo-incisive length	26.1, 24.8		—	—
Upper molar row	4.1, 4.0		4.34 (3.95–4.80) (67)	4.35 (4.0–5.1) (n = 43)
Height of braincase	8.1, 7.6		—	—
Intraorbital width	4.4, 4.3		4.2 (3.70–4.95) (n = 67)	4.2 (3.90–4.75) (n = 43)
Zygomatic breadth	13.7, 12.7		12.6 (11.30–13.95) (n = 66)	12.3 (11.25–14.00) (n = 33)

^aSpecimens CM 113707 and 113708.

^bAfter Van der Straeten and Verheyen (1978).

species as separate from *M. daltoni*, only one locality was from the Accra Plains (Achimota). Both of these new specimens display the characteristic "white irregular spot . . . on the chest" and were caught "in human dwelling or in their immediate surroundings" (Van der Straeten and Verheyen, 1978:35).

DISCUSSION

Most of the new distributional records of species reported for the Accra Plains are additional zoogeographical evidence for the presence of Guinea and Sudan savanna faunal elements on the Accra Plains with some additional high forest species. These records support Booth's (1959:35) hypothesis that "the savannah element of the fauna is not a relic, but a group of invading species which has arrived on the Plain from the north and east" and that "the savannah environment may be comparatively new to the Accra Plain, and represents a recent change in vegetation due either to climatic changes or to human activity, or both." Livingstone (1975) described climatic changes in Africa. There have been several moist periods, one prior to 30,000 YBP and another from 12,000 to 7000 YBP. Since 3000 YBP conditions have been dry, probably aggravated by human influences in many areas. Talbot (1981) found additional evidence of drought conditions and dry winds from 4500 to 3800 YBP, based on the presence of an aeolian sand layer and a dune ridge along the coast of the Accra Plains. However, Robbins (1978) argued for a mostly anthropomorphic origin of the savanna vegetation of the Dahomey Gap, the break in the forest zone of West Africa between the Volta and the Niger rivers, on the basis of fertile soils and forest remnants. He concluded (Robbins, 1978:174) that instead of the Dahomey Gap, "both the Volta and Niger rivers have been major factors influencing mammal distribution, with the Niger being the more important (33.4% as opposed to 17.5% for the Volta)."

Dry conditions may have allowed typical Guinea savanna species like *Crociodura lamottei*, and good dispersers like the bats *Eptesicus guineensis*, *E. capensis*, *Nycticeinops schlieffeni*, and *Pipistrellus aegyptius* to reach the Accra Plains from the Guinea savanna via the Dahomey Gap and along the Volta River valley. Moist periods may have caused the expansion of rainforest from the Akwapim escarpment down into the Accra Plains. This may have led to the establishments of species like *Crociodura buettikoferi*, *C. nigeriae*, and *Myotis bocagei* as well as other species caught during this study but not discussed above, such as *Epomops franqueti*, *Myonycteris torquata*, *Hipposideros beatus*, *H. cyclops*, *Glauconycteris poensis*, and *Hylomyscus alleni* (Decher, 1996). These forest species remain today in the extensive dry forests such as Pinkwae Forest and in high forest remnants such as Adumanya Sacred Grove, after the climate became drier, or after land use and deforestation in the surrounding areas increased. The finding of *Otomops* in northern Ghana may be an indication that many bat species and especially those with high aspect ratios, that is the ratio of wingspan squared to wing area (O'Shea and Vaughan, 1980), should be expected to be more widely distributed than conservative estimates from existing localities in central and eastern Africa might indicate.

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APPENDIX

Gazetteer of Collecting Localities from Ghana

BAR = Brong Ahafo Region		NR = Northern Region	
CR = Central Region		UWR = Upper West Region	
ER = Eastern Region		VR = Volta Region	
GA = Greater Accra Region			
Achimota	GA	5°37'N	0°14'W
Adumanya Sacred Grove	GA	5°54'N	0°04'E
Anomabu (or Anamabu Castle)	CR	5°10'N	1°07'W
Bimbila	NR	8°52'N	0°04'E
Boti Falls	ER	6°12'N	0°14'W
Bungweli (Mole National Park)	NR	9°41'N	1°52'W
Doryum (Doyum)	GA	5°54'N	0°01'E
Butre	WR	4°49'N	1°55'W
Gambaga	NR	10°31'N	0°22'W
Kpong Agricultural Research Station	ER	6°08'N	0°04'E
Kokofu	BAR	7°43'N	0°53'W
Kukurantumi	ER	6°12'N	0°22'W
Legon, Botanical Garden	GA	5°40'N	0°12'W
Mamobi, Accra	GA	5°36'N	0°11'W
Odomi Jongo	VR	8°19'N	0°31'E (?)
Pinkwae Dry Forest	GA	5°45'N	0°07'W
Pirisi	UWR	10°07'N	2°27'W
Pulima	UWR	10°51'N	2°03'W
Sakpa	NR	8°52'N	2°21'W
Saruwi River, Jukwa	CR	5°16'N	1°20'W
Shai Hill Resource Reserve, NE ("Pillar 14")	GA	5°57'N	0°04'E
Shai Hills RR, NW	GA	5°53'N	0°03'E
Shai Hills RR, SW	GA	5°57'N	0°04'E
Yendi	NR	9°25'N	0°04'W

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———. 1923. The fauna of the Ardyn Obo Formation. *American Museum of Natural History Novitates*, 98:1–5.

- 3) Same authors plus a third author—repeat all authors:

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- 4) Chapter in an edited volume:

RAUSCH, R. L. 1963. A review of the distribution of Holarctic mammals. Pp. 29–43, in *Pacific Basin Biogeography* (J. L. Gressitt, ed.). Bishop Museum Press, Honolulu, Hawaii.

- 5) Unpublished dissertation:

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- 6) Book:

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THE CARNEGIE
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HISTORICAL DOCUMENTATION AND ARCHAEOLOGICAL
INVESTIGATION OF CODRINGTON CASTLE, BARBUDA, WEST INDIES

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Curator, Section of Anthropology

ABSTRACT

Codrington Castle was Barbuda's principal structure for almost two centuries (1680s-1870s) while the island was leased by the Codrington family. The building no longer exists because it was razed near the turn of the 20th century. Analysis of historical documents determines the Castle's position, configuration, and architecture; analysis of archaeological data verifies its chronology, construction, and renovation. The study concludes that: (1) three rectangular buildings sequentially occupied the same location; (2) these structures had different long-axis orientations; (3) the Castle's functions included defense, storage, administration, and habitation; and (4) an expansive subsurface archaeological feature delineates the extent of the second Castle. Descriptive analysis of the ceramics distinguishes imported wares from Afro-Caribbean pottery and defines three intermediate ceramic categories in which the syncretism of two pottery-making traditions is correlated with the ethnicity of the potters and manufacturing locations. Lithic artifacts are interpreted as evidence for direct exploitation of West Indian chert sources during the historic era or, alternatively, for the recycling of prehistoric artifacts by historic inhabitants. Manufacturing timespans and stratigraphic positioning of imported ceramic, glass, and kaolin pipe artifacts corroborate Codrington Castle's duration of occupation as determined from historic records. The Castle exemplifies Barbuda's role in provisioning the vast sugar estates that were the basis of the Codrington family's wealth.

INTRODUCTION

Background

Codrington Castle commanded land and water approaches to Codrington village from a tactically strong defensive position midway along the east shore of a large lagoon in the western part of Barbuda. The Castle dominated the village landscape for about 220 years, from its initial construction in the 1680s, during the earliest years of the Codrington family's leasehold, until the deteriorating building ultimately was razed near the beginning of the 20th century.

Although documents attest to the Castle's prominent role in Barbuda's history, they contain relatively few details about the building's architecture and reveal only limited information about its functions. This paper presents the results of research on the Castle's location, construction, configuration, architecture, and chronology using evidence derived from historical documents and data from archaeological field work. The study discusses the anthropological implications of (1) the Castle's ceramic artifacts, particularly their place of manufacture and the ethnicity of the potters, and (2) its lithic artifacts, particularly New World and Old World sources and the possible historic period reuse of prehistoric artifacts. The paper concludes that the Castle's functions changed through time in response to shifting historical trends in the West Indies, that buried structural features define the Castle's layout, that Codrington Castle's relationship with other sites on Barbuda is documented by historic records and recovered artifacts, and that the Castle

and Barbuda were closely tied to the economy of Codrington sugar estates elsewhere in the West Indies.

The Codringtons in the West Indies

Barbuda and the Codrington family are intimately linked. The Codringtons first settled in the West Indies in 1628 at Barbados (500 km SSE of Barbuda), shortly after its colonization by the English, and the family soon attained prominence among planters of that island. By the early 1680s, they leased their Barbados estates to other planters, moved north to the Leeward Islands, and took up residence in Antigua (Tweedy, 1981:10–12; Harlow, 1990). The family acquired landholdings on Antigua and St. Kitts (Fig. 1), developed them into major sugar plantations, and soon accumulated great wealth from the sugar industry. During this period they also leased Barbuda. The Codringtons' premier estate and principal residence was Betty's Hope plantation in Antigua (Carstensen, 1993; Goodwin, 1994). The earlier members of the family, those who first emigrated to the West Indies and those born there, lived most of their lives in the islands; but their descendants resided almost exclusively in England at the family estate of Dodington in Gloucestershire. The Codrington family thus exemplifies the trend toward absentee ownership that became so prevalent among the wealthy West Indian sugar planters.

The third Christopher Codrington (III; to distinguish him from his grandfather and father with the same name) exemplifies the involvement of the Codrington family with the West Indies. Born in Barbados in 1668, he left there to attend school in England, fought with distinction for England in the Flemish war in Europe, returned to the West Indies upon being appointed Governor of the Leeward Islands in 1699 (succeeding his deceased father), became leaseholder of Barbuda, led military campaigns against the French in the Lesser Antilles, and retired to a scholarly life at the Codrington estate of Consett in Barbados where he died in 1710 (Tweedy, 1981:12–13; Harlow, 1990). He was the last of the West Indian-born Codringtons to die in the West Indies. His will provided for the creation of what eventually became Codrington College at Consett plantation (Oliver, 1894, I:150–151; Holder, 1988).

The Codringtons leased Barbuda from the British Crown for about 200 years. Details concerning the family's initial leasehold are sketchy (and complicated by earlier leases to others) but it may have begun as early as 1669 or 1677 (Harlow, 1990:15, 190), while the Codringtons still resided in Barbados. They certainly possessed Barbuda by 1684, the year a new lease giving them sole control was granted to two brothers, Christopher (II) and John Codrington. Christopher (III) inherited the lease to Barbuda from his father (Christopher II); the family retained control through a series of leases from the Crown until 1870. The only break in the Codrington family's possession of Barbuda was a 15-year sublease, beginning in 1746, to Colonel Samuel Martin and William Byam of Antigua (Tweedy, 1981: 26).

Economy of Barbuda

Barbuda is a carbonate island of low relief in the Leeward Islands, the northern sector of the Lesser Antilles island chain that borders the eastern Caribbean Sea, separating it from the Atlantic Ocean. The nearest neighboring island, Antigua, lies some 40 km south (Fig. 1). Barbuda's surficial geology consists of Pliocene

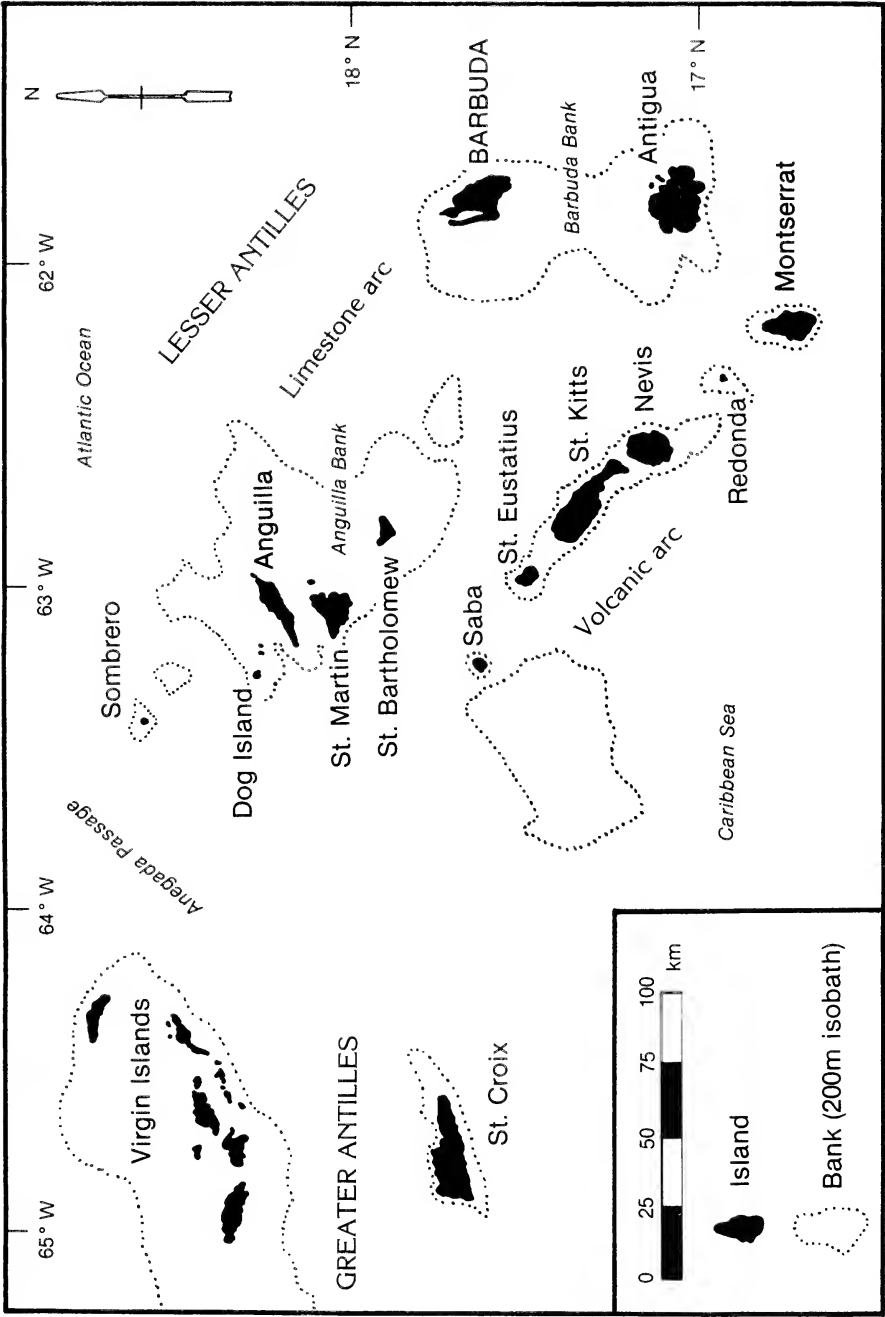


Fig. 1.—Barbuda is located in the northern Lesser Antilles (Leeward Islands) about 40 km north of Antigua.

to Pleistocene limestone formations and Holocene sand deposits (Brasier and Mather, 1975; Brasier and Donahue, 1985). Land area is about 160 km² (62 mi²). The island has very shallow soils, limited rainfall, and mainly xerophytic vegetation, but it is surrounded by very productive marine environments ranging from shallow bottoms to extensive reefs (Harris, 1965; Watters et al., 1992:15–25).

Barbuda's climatic and edaphic limitations precluded the cultivation of sugar, tobacco, or other commercially important crops in the colonial era (apart from sporadically grown cotton); these factors also thwarted commercial agricultural enterprises in more recent times (Berleant-Schiller, 1978). Since Barbuda was unsuited for cultivation of plantation crops, its acquisition by the Codringtons may seem incongruous. Barbuda, however, was an integral part of the broader economy of the Codrington family's West Indies holdings. It served as an important provisioning island, supplying a range of commodities needed by the Codrington sugar estates and selling surplus staples to other plantations. Hides, meat, corn, wood, charcoal, lime, turtles, fish, and livestock (horses, mules, cattle, swine, goats, and sheep) were among its exports (Watters, 1980b:125). Boats built by Barbudans brought supplies to that island, transported hogsheads of Codrington sugar around the coast of Antigua, and also carried goods to other islands in the Lesser Antilles.

Codrington Village and the Castle

The village of Codrington, located midway on the east shore of the expansive lagoon on the west side of Barbuda (Fig. 2), was the island's administrative center throughout the Codrington leasehold. All slaves, overseers, and managers were required to reside in the village. Industrial facilities such as the tannery were located there. The village was enclosed by stone walls that existed until the 1970s, when they were torn down and crushed for road-building material. Gate pillars and remnants of some walls remain today (Fig. 3). The narrow paths winding among walled or fenced houseyards identify the older sections of the village; they stand in sharp contrast to the gridded road plan in newer parts. Extant place names (see Berleant-Schiller, 1991), such as Mulatto Quarter, may derive from the Codrington period as well.

Codrington Castle was referred to simply as the "Castle" throughout the Codrington leasehold. Surface remains surviving the structure's demolition at the beginning of the 20th century are few, but the Castle's location is known to Barbudans because of Castle Well, which today remains the most conspicuous structural remnant of the razed Castle. The few surface remains at Codrington Castle contrast markedly with most of Barbuda's other historic sites (Fig. 2), where standing structures generally are preserved (Watters, 1980b; Watters and Nicholson, 1982).

Documents confirm that Castle Well existed as a traditional water source for Barbudans at least as early as 1787 (Tweedy, 1981:170, 199, fn. 15); its reputation "never to have run dry" (Hall, 1971:70) is a meaningful attribute on this drought-prone island. In 1978–1979, during the author's initial field work on Barbuda, Castle Well was still being actively used by residents of Codrington as a water source for themselves and especially their livestock, despite the water's relatively high salinity (Mather, 1971:appendix 2, Well 31). A piped water system installed in the village in the 1980s so reduced the inhabitants' reliance on Castle Well that by 1992 the wellhead had been capped by a concrete cover (Fig. 4).

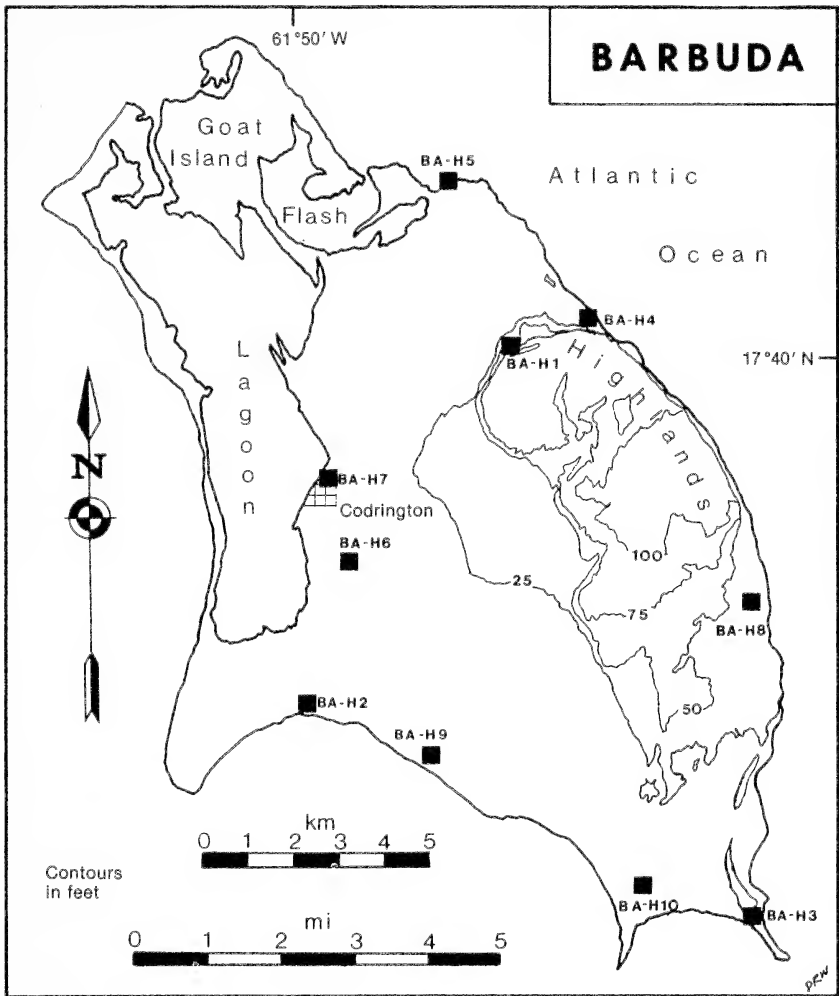


Fig. 2.—Historic sites of Barbuda. Codrington Castle (BA-H7), Highland House (BA-H1), River Fort (BA-H2), Spanish Point structure (BA-H3), and Coco Airstrip lime kiln (BA-H10) are discussed in the text.

DOCUMENTARY EVIDENCE

Sources

Architectural information about Codrington Castle is derived from maps, charts, drawings, documents, the correspondence of the Codrington family and its employees on Barbuda, and accounts of visitors. The following sections review the data derived from the written and pictorial documents; the final section analyzes these data as they pertain to the Castle’s location, position, configuration, orientation, and architecture.

However, the Codrington Papers, which undoubtedly would have been a most valuable documentary source, are no longer available for scholarly use. The documents, which had been accumulated by the Codringtons at Dodington estate,



Fig. 3.—One of the remnant limestone block pillars of the gateway through the wall on the north side of Codrington village. Low Pond, still enclosed by its historic stone wall, is visible in the background, with the lagoon behind.

were loaned by the family to the Gloucestershire Records Office and thus were accessible to scholars until 1980, when the family requested their return. The original documents subsequently were purchased by an anonymous buyer at an auction in London; since then they have been inaccessible.

Microfilms of selected documents from the Codrington Papers were made by the Gloucestershire Records Office. Two scholars, Riva Berleant-Schiller and Margaret Tweedy, who examined the original or microfilmed documents during their own research on other topics, generously shared information they obtained regarding Codrington Castle with the author. Tweedy's (1981) thesis, although it is temporally restricted (1738–1833) to about one-half of the leasehold, is an especially valuable source of information about the Castle. Selected documents from the Codrington Papers are available in a limited-distribution folio produced by the Devonian Foundation (1988), a copy of which was examined by the author at the Museum of Antigua and Barbuda. While these sources provide important, albeit selective, documentation regarding Codrington Castle, there is no doubt

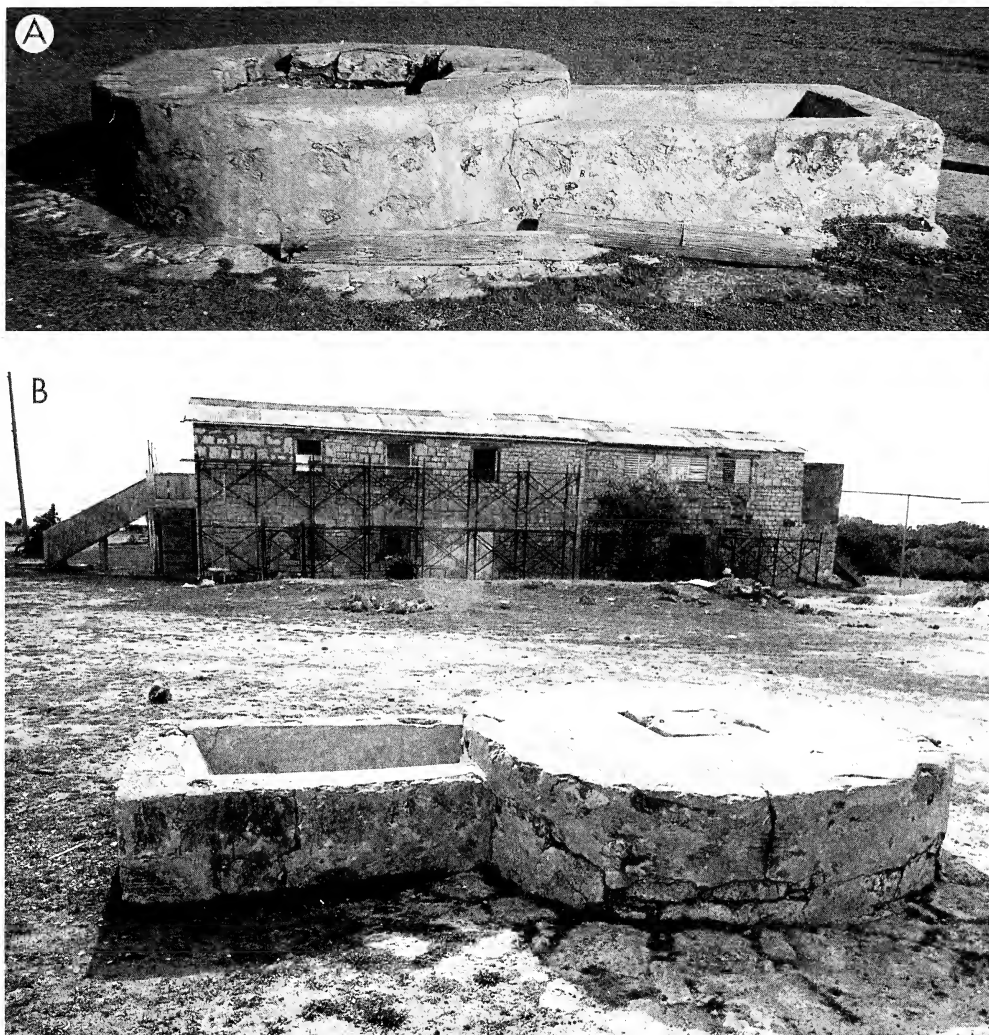


Fig. 4.—Castle Well as it appeared in 1979 (A) and 1992 (B). Note position of historic Castle Well in relationship to the present ginney building (cf. Fig. 10, 11).

that additional information could be derived from the Codrington Papers were the documents made available in their entirety.

Maps and Charts

Five facsimile maps of Barbuda were examined in the Devonian Foundation folio. The oldest, ca. 1710, is a small map inset in one corner of a larger plan of Betties Hope (original spelling) estate on Antigua. Reproduction quality is poor but a structure is vaguely discernible near the lagoon on Barbuda. Four other maps, all hand drawn, are attributed to the interval between the 1750s and 1780s. They are consistently inaccurate in their renderings of the overall configuration of Barbuda, most notably in their depiction of an island much wider (east to west)

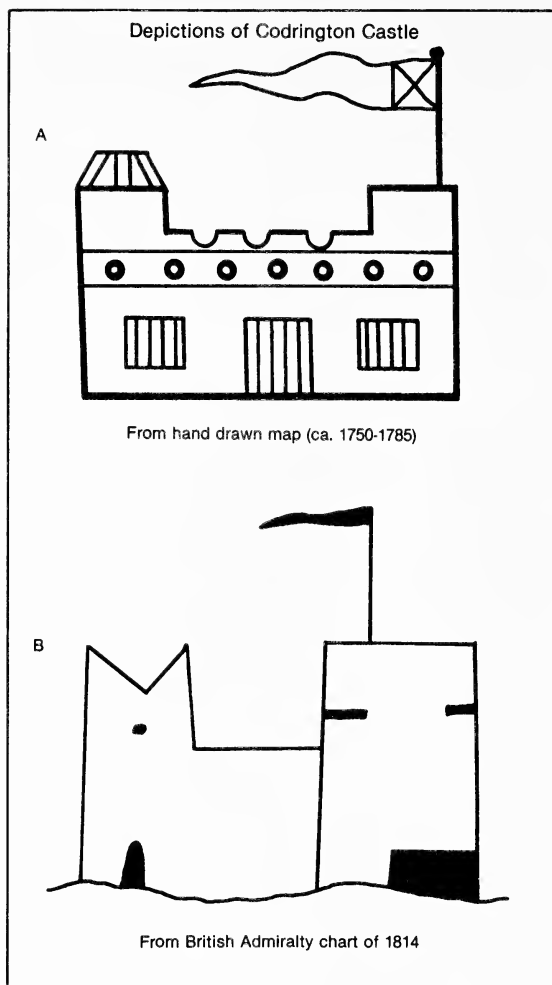


Fig. 5.—Depictions of Codrington Castle on maps and charts.

than in actuality. These maps likely were provided to the Codringtons (then residing in England) by one or more managers of Barbuda to assist the family in its efforts to administer this remote island by correspondence.

Each of the four maps locates the Castle (labeled as such and depicted by a prominent structure) midway on the east shore of the lagoon (called the Lake or Pond). The renderings display some recurrent features although the buildings are not consistent or uniform in specific details. The common features are a tower on each end, embrasures atop the wall, a prominent flagstaff and flag, and a central door flanked by windows or shutters (Fig. 5A; composite drawing of individual depictions). The four maps consistently portray only the south-facing exterior wall, seen from ground level, and they presumably depict the Castle's main entrance. Since this perspective masks the side and rear walls, it is not possible to gain an impression of the Castle's depth nor to judge the relative lengths of its walls.

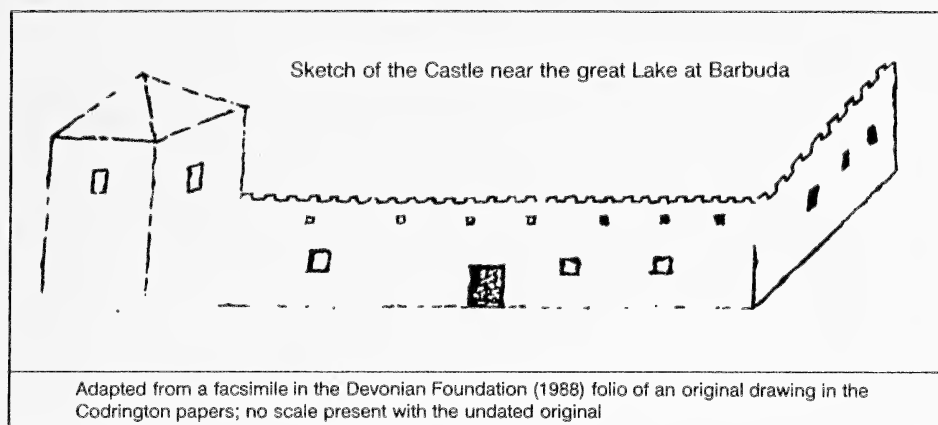


Fig. 6.—Rendering of the exterior of two walls at Codrington Castle. The tower and entrance denote the south wall.

Barbuda is accurately rendered for the first time in an unnumbered British Admiralty chart dated 1814 and entitled “The Island of Barbuda, Surveyed by Capt. Decker R. N. 1813.” The wreck of the warship *H. M. S. Woolwich* in 1813 on reefs north of Barbuda (the wreck site is shown on the chart) prompted this survey. A building (tiny in size and again drawn from ground level) having two towers and a flag and flagstaff (Fig. 5B) is shown in Codrington village, and the word “Castle” is printed on the chart above the building (Admiralty Hydrographic Office, 1814). The illustrator depicted a decidedly European-appearing structure. The next chart of Barbuda, based on an 1848 Admiralty survey, shows in plan-view a number of individual structures in the village. A rectangular building, with its greatest length oriented north–south, is shown in the proper location for the Castle but it is not labeled as such, and no flagstaff, towers, or crenelated walls are portrayed. The phrase “Castle Landing,” applied to the nearby wharf, is the only allusion to Codrington Castle (Admiralty Hydrographic Office, 1850). Recent maps of Barbuda (Directorate of Overseas Surveys, 1970) neither depict nor reference the Castle.

Drawings

Facsimiles of two drawings in the Devonian Foundation folio (1988) depict architectural elements. The first, labeled “Sketch of the Castle near the great Lake at Barbuda,” shows the exterior of two of the building’s walls, one tower with a peaked roof, a central door in one wall, windows in both walls, and a series of small embrasures atop the walls with possible gun ports beneath them (Fig. 6). The wall facing the viewer is longer than the side wall; however, the side wall’s apparent shorter length may be a distortion of the depth perspective. Orientation of the structure with respect to cardinal directions or to the lagoon cannot be discerned from this drawing.

The second drawing (untitled and undated) depicts one large structure and numerous small buildings, the latter having gabled roofs. Based on the quantity of buildings and their proximity to “The Lake” (so labeled and showing a ship), this drawing must be a map of Codrington because the village was the only

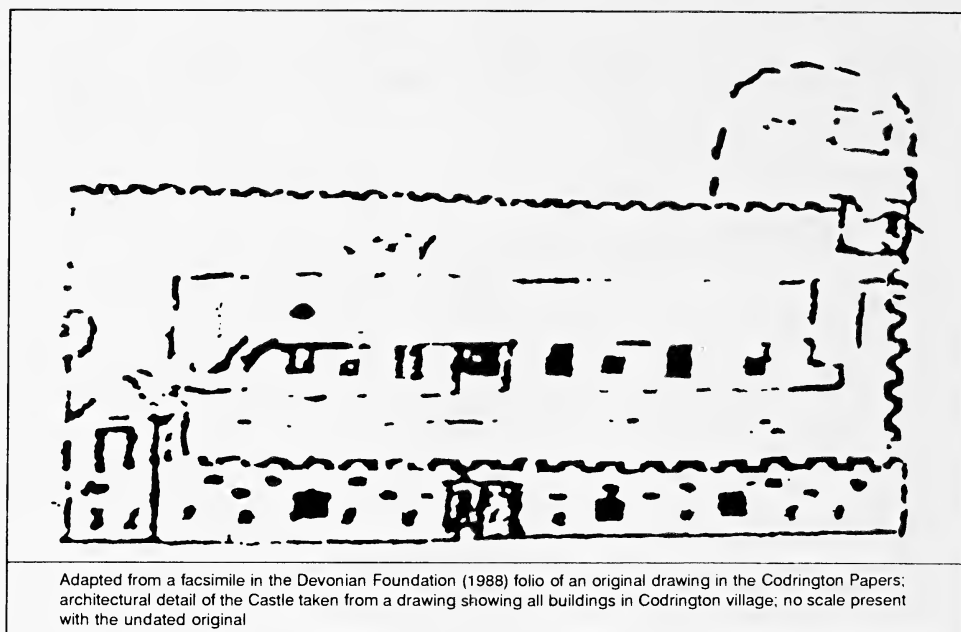


Fig. 7.—Detail of Codrington Castle extracted from a larger map depicting the village of Codrington. The exterior of the south wall (at the bottom of the illustration) is drawn from ground-level perspective and incorporates a tower and the main entrance.

habitation place on Barbuda. Buildings are designated by numbers but the facsimile lacks the key that signifies their meaning.

The large structure represents the Castle and incorporates a combined front view and partial planview (Fig. 7). The west wall of the building parallels the east shore of the lagoon, thus providing its orientation. The rectangular building's long axis is oriented east–west; its front and rear walls are more than twice the length of the side walls (again, possibly distorted by perspective). The southward-facing exterior front wall displays one tower, embrasures, windows, and a central door. The other walls are shown only in planview but they continue a crenelated pattern indicating embrasures. The artist seemingly attempted to portray the interior of the rear (north) wall by vague renderings of some windows and possibly a door. A semicircular pattern is depicted on the exterior of the building's north-east corner; the intended function is uncertain but it may be a fenced corral.

Watercolor

Codrington Castle appears on the left edge of a watercolor, entitled “A View of the Island of Barbuda,” painted by N. James and dated June 1818. The artist may have been related to John James, who then was serving as manager and attorney for Barbuda (Tweedy, 1981:appendix III). The visible segment of the Castle includes part of a wall from which projects what appears to be one side of a bastion (Fig. 8). A crenel and merlon battlement tops the wall and bastion.

The building displays no features, such as doors or windows, by which to estimate wall height but a rough scale is provided by the portrayed animals and humans. Wall height of between 5 and 7 m (ca. 15–20 ft) can be extrapolated



Fig. 8.—Watercolor of Codrington village depicting (left side) part of the Castle, ca. 1818. [Used with the permission of Hamilton College, New York.]

from two deer standing some distance beyond the bastion. Foreground people and animals allow for a height estimate of between 3 and 5 m (10–15 ft).

The house in the center background, serving as the focal point for the painting, depicts the west face of what has more recently been called Warden's House (discussed below). A road from the lagoon leads to the house; the Castle is appropriately situated on the north side of that road. Therefore, the visible part of the Castle is the eastern end of its southern wall; the bastion forms the southeast corner. In the far background, between the Castle and the main house, are individual structures representing slave quarters. The depiction of the two deer is noteworthy because the Codringtons imported European fallow deer, *Dama dama*, to Barbuda for hunting. They survive on the island today (Chapman and Chapman, 1980:119–120; Chapman, 1996).

Written Documents

Henri de Ponthieu, an amateur botanist who visited Barbuda in 1783, specifically mentions the Castle's elevated platform and ground-level rooms. His suggestion that rooms be built on that platform, supposedly to provide a good view of activities in the village, most likely was prompted by the dampness he experienced while staying in the Castle's lower rooms (Tweedy, 1981:169–170).

Two accounts written about 50 years later provide more details about the layout of Codrington Castle and other buildings located nearby. The first, from 1834, states:

An old dilapidated tower, with several smaller erections attached to it, occupying one corner of an extensive parallelogram, formed by high walls, constitutes 'the castle.' The tower is said to have been built in the days of buccaneering notoriety, and it hath features that correspond with its reputation. One large room occupies the upper part of it, to which access is gained by a ladder, a convenience that may be dispensed with at discretion to avoid unwelcome visitors. Inside the enclosure, there is a kitchen and other offices, and a raised terrace round the wall, and a well in the centre, the whole affair indicating strength and security; qualifications, which are tacitly implied to be useless by a more modern formal farm-house looking building, which stands in the rear of it, where the viceregent is domiciled. The hospital, stables, and artificers' stores lie detached in different directions. (Wentworth, 1834:[II]242).

The second description appears in a report (cited in Hall, 1971) by two Antiguan magistrates, Graeme and Walker, who visited Barbuda in May 1840. Excerpts from their report state:

In the village itself the most impressive building was the 'Castle', rectangular with towers at the north-east and south-west corners 'connected by substantial stone-walls with embrasures'. In the interior courtyard there was a well, said never to have run dry; and in the southern quarter a house had been built as an overseer's quarters. Near to the Castle were the Manager's house and the farm buildings, all of stone. There was also another building which served as a chapel and schoolroom. 'In arrangement and appearance they reminded us more of similar establishments at home [presumably meaning Great Britain] than of a tropical plantation.' The village also contained the labourers' houses. These were generally of 'wattle-and-daub' built on wooden frame-posts and roofed with thatch made of long, tough 'sage grass'. They appeared neat and

comfortable, and each house stood in its own yard, enclosed by a wattle fence for protection against cattle roaming at night. (Hall, 1971:70).

Descriptions of the Castle's configuration and layout are rare, but references to its condition are more numerous and cover a longer timespan. Manager Simon Punter wrote in 1743 that he had put the Castle in the "best posture of Defence it will admit of" (Tweedy, 1981:35). Benjamin King in 1746 commented that the "old Castle" was a place of "no Deffence" with walls only three feet thick, and he suggests that improvements were needed (Tweedy, personal communication, 1991). Henri de Ponthieu's stay at the Castle indicates it was habitable in 1783, but he regarded the structure as being virtually useless against an enemy, at least those having European weapons (Tweedy, 1981:35). In 1813, Captain Greville, an officer from the wrecked H. M. S. *Woolwich*, mentioned an "...old dilapidated castle, said to have been built by the Buccaneers. . ." and also remarked that "this piece of antiquity has nothing particular to recommend it. . ." (Southey, 1968: [III]523–524; cf. Oliver, 1894:[I]cxlix). Coleridge (1832:255) wrote that a carriage dispatched from the Castle picked up his party during its visit in 1825. Statements in the Coleridge (1832:257–260) account imply that his party was lodged and fed at the Castle, but he provides no information about its condition (apart from it being mosquito infested).

The Castle is referred to in an 1835 agreement between the resident manager, acting on behalf of the Codringtons, and the newly emancipated Barbudans, whereby certain individuals were allocated small provision grounds within a 1.5-mi radius of the Castle (Hall, 1971:67). In 1837, a Codrington attorney visiting from Antigua wrote that "The Buildings at the Castle, formerly a strong and secure place, are now little better than a Ruins and unfit to receive, and to store a crop" (Liggins, 1837:5).

Liggins' unfavorable characterization of the Castle tends to be supported by Wentworth's (1834) nearly contemporaneous account. Yet, soon thereafter, in 1840, magistrates from Antigua reported that an overseer lived in the Castle and they asked permission to hold their session in one of its rooms (Hall, 1971:70–71), thus indicating the building was still being used. In 1854, in his application to the Crown for renewal of the lease, Christopher William Codrington mentioned that during a visit to Barbuda around 1843, he found almost all the buildings had been destroyed by an earthquake, including the Castle and fortifications having been razed to the ground, and that he had ordered them to be repaired (Hall, 1971:76). A visitor in 1850 was offered use of a "turret" for lodging; but the turret was a room detached from the manager's house (cf. Fig. 8) and could not have been a tower in the Castle (Day, 1852:[II]285). The Castle was extant in some form in 1870 because the Crown reserved parts of the building for its own use, as one stipulation in a new lease issued to Hopkins and Cowley, following the Codrington family surrender of its lease that same year (Hall, 1971:89).

Visitors' accounts after about 1870 no longer explicitly mention the Castle and, instead, refer most often to the "great house" in the village. Ober, who visited Barbuda in 1877 while collecting birds for the Smithsonian Institution (Lawrence, 1879:232), arrived "... at the 'great house,' built in the flourishing times of the Codringtons" (Ober, 1904:310). During Hill's (1898:322) visit, the only white man on the island resided in the great house. This still extant great house, depicted as the central building in the 1818 watercolor (Fig. 8), lately has been called "Warden's House" and "Government House." The lack of reference to Codring-

— To help ourselves we must help each other —



The BARBUDA VOICE

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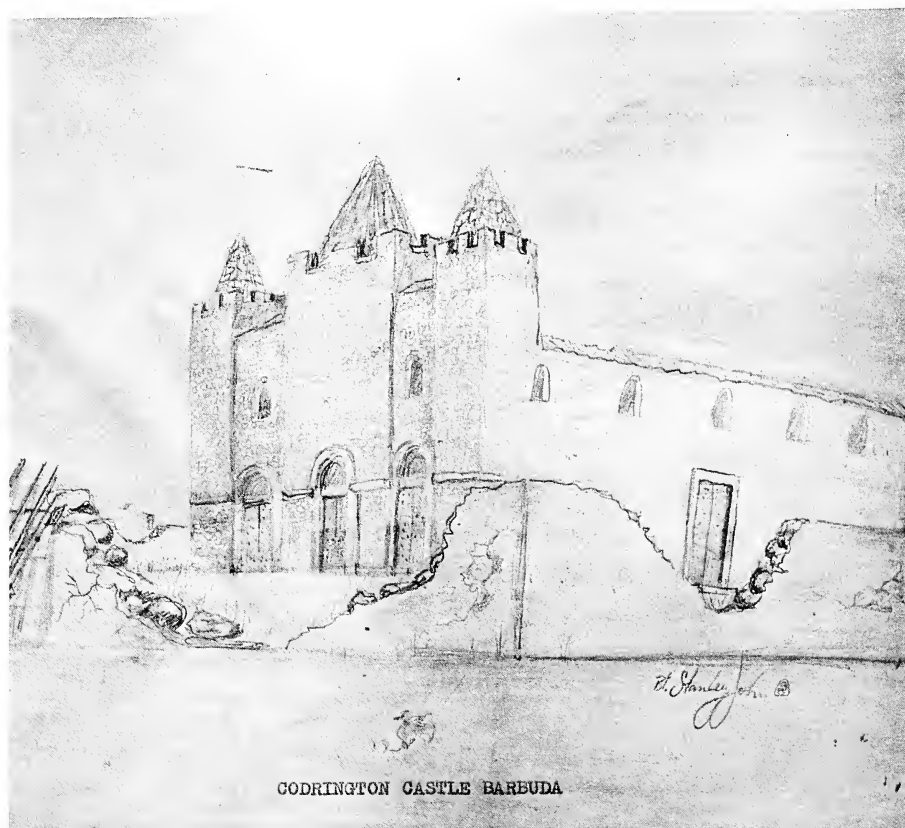


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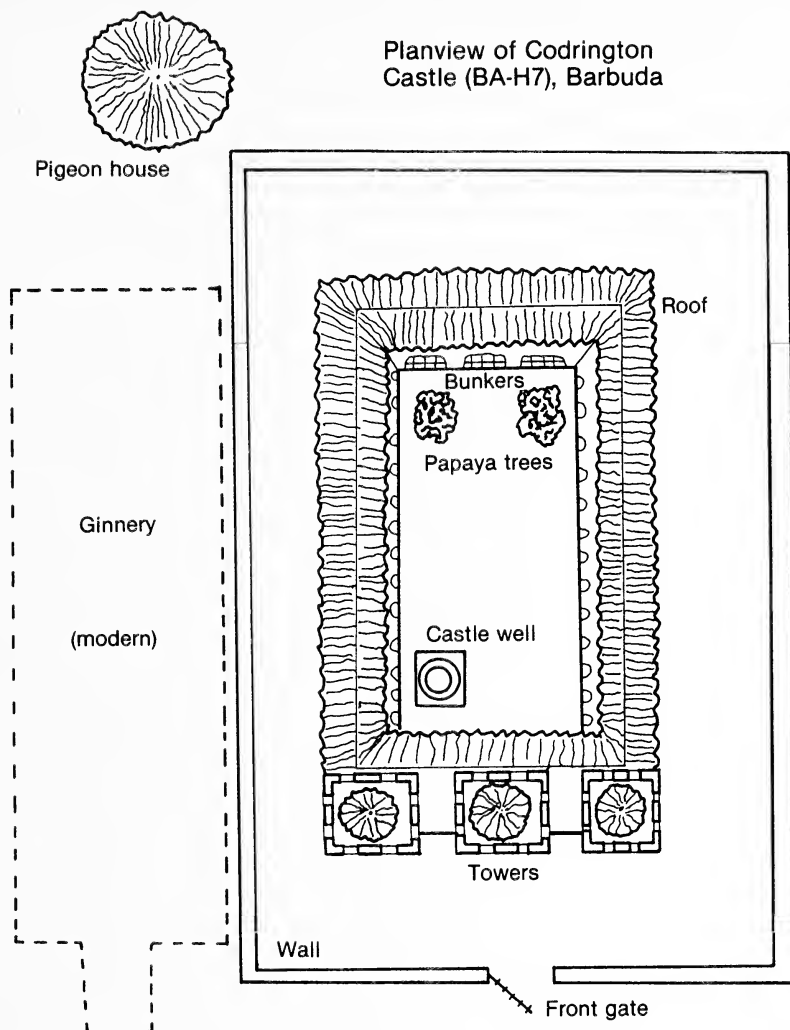
CODRINGTON CASTLE BARBUDA

Fig. 9.—Illustration of Codrington Castle appearing on the cover of *The Barbuda Voice*; rendering based on the recollections of Reverend Reynold Walbrook. [Used with the permission of Russell John, editor, and Stanley John, illustrator.]

ton Castle by visitors in the late 19th century implies the structure either no longer existed or was not worthy of comment.

Modern Rendering

The Barbuda Voice, the newspaper of the Barbuda's United Descendants (BUD) Society headquartered in the Bronx, New York, published information about Barbuda from 1969 to 1990. One early issue (*The Barbuda Voice*, 1971) has an illustration of Codrington Castle on its cover (Fig. 9), a planview of the structure



Adapted from *The Barbuda Voice*, vol. 3, no. 22, p. 2, July 1971
(no scale present on original illustration by Stanley John)

Fig. 10.—Planview of Codrington Castle with architectural details based on Rev. Walbrook's recollections (adapted from *The Barbuda Voice*).

(Fig. 10), and general information on the site, based on the childhood recollections of Reverend Reynold Walbrook. Russell John, editor of *The Barbuda Voice*, interviewed Walbrook for the Codrington Castle issue; Stanley John prepared the artwork. Walbrook's obituary (*The Barbuda Voice*, 1990) states he was born on Barbuda in 1894 and emigrated to the United States in 1918.

Walbrook's recollections bear on the issue of when the Castle was razed. The critical point is whether he actually observed a still-extant Castle during his childhood. Although the article does not state that his recollections are based on his own observations, both Stanley and Russell John (personal communication, 1991)

are convinced, based on their memories of the interview and the preparation of the artwork, that Walbrook's remembrances are derived from his personal observation of the Castle as a child, rather than information told to him by others. This line of reasoning implies that the building existed, in some form, until the late 19th and perhaps the early 20th century.

In the cover illustration, the exterior of the Castle is portrayed in a good state of repair, but a surrounding stone wall is damaged (Fig. 9). The cover illustration and planview show three square towers along the south wall, with each tower being topped by a crenel and merlon parapet and a conical roof. The walls have no embrasures but are roofed. In the illustration, the south wall of the building contains three arched doorways, assumed to represent the main entrance, and the east wall has one rectangular doorway.

The planview provides more details about the Castle and its orientation and positioning with respect to the modern ginnery (Fig. 10). The rectangular Castle has its greatest length oriented north-south and its front wall (main entrance) facing south. A rectangular open area is delineated by the interior walls of the Castle. Visible within that open area are Castle Well, near the southwest corner, and two papaya trees close to the north wall. Three "bunkers," said to have housed slaves for punitive measures, are located in the interior of the north wall. Another open area intervenes between the exterior of the Castle and the wall that surrounds the building. A pigeon house is positioned beyond the northwest corner of the surrounding wall.

Analysis of Historical Documentation

Historical documents confirm the Castle's location within Codrington village and its position midway on the east shore of the lagoon. It is usually depicted as rectangularly configured with a prominent south wall. Codrington Castle was constructed of limestone, the only rock available locally, as are all of Barbuda's extant historic period buildings (Watters, 1980b; Watters and Nicholson, 1982).

Architectural features that recur with regularity in these accounts include crenelated walls, one or more towers (sometimes roofed), one principal entry door, and various windows. Features noted less frequently include an elevated platform or raised terrace, bastion, gunports, bunkers, and flagstaff. Within the confines of the Castle were located a well, kitchen, offices, ground-level rooms, and papaya trees. Beyond the Castle walls were a pigeon house, an offset low stone wall, and an attached semicircular feature likely to be a corral. Overall, these descriptions and illustrations of Codrington Castle evoke an image of a very substantial stone structure having walls and battlements almost medieval in appearance.

The documents are discordant with regard to one aspect of Castle construction; that is, its orientation. Older drawings (Fig. 6, 7) orient the rectangular building east-west, with the south wall (and north wall, when visible) being considerably longer than the east and west walls. Yet, Walbrook's planview (Fig. 10) orients the structure along the north-south axis with correspondingly longer east and west walls, and the 1848 chart is in accord with this orientation. The other maps and charts have neither depth perspectives nor planviews to help resolve this matter; written accounts do not discuss the Castle's orientation. Despite the ambiguity about relative length, the south wall most often is shown as the principal entrance to Codrington Castle in these illustrations.

Apart from Benjamin King's statement about the Castle's walls being three feet

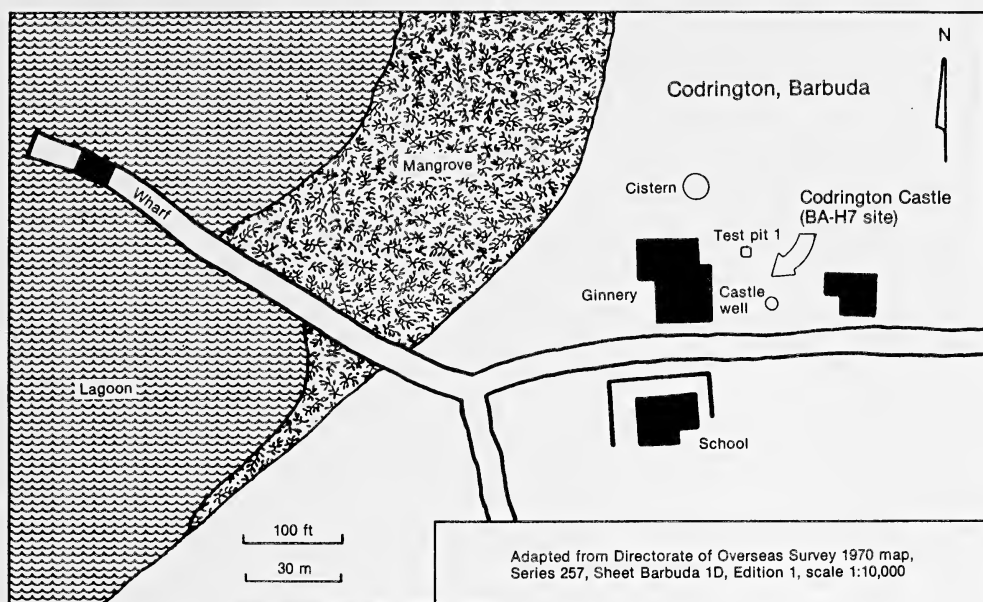


Fig. 11.—The Codrington Castle site in relation to the lagoon and wharf and to historic (Castle Well) and modern (ginney) structures.

thick (Tweedy, personal communication, 1991), no quantitative data about the building's measurements or area were obtained from the written accounts, and the maps, charts, and drawings contain no scales for extrapolating dimensions. Yet, certain qualitative statements, such as an "impressive building" or "high walls," contained within the historic documents imply that the Castle was a substantial structure, and an estimated wall height of 15 ft (range of 10–20 ft) can be deduced from the watercolor.

The historic documents, despite their various constraints, are significant for interpreting the architecture, structure, and appearance of the Castle because none of its above-ground features, except for Castle Well, survived the razing.

ARCHAEOLOGICAL EVIDENCE

Survey and Excavation

Codrington Castle, designated as site BA-H7, is located at UTM coordinates PQ243507 (Directorate of Overseas Surveys, 1970). The site area extends outward in all directions from Castle Well.

The site's surface was examined and one test pit excavated in 1978–1979, during the course of other archaeological research on Barbuda (Watters, 1980a). This reconnaissance covered the area inland from the mangrove-bordered lagoon to around Castle Well, the ginney, and the cistern (Fig. 11). Historic and modern artifacts were intermingled on the surface; the only artifact concentration (remnants of a shallow dump) occurred near the mangrove shoreline west of the cistern. The mixed distribution of the surface artifacts precluded an accurate determination of the Castle's extent during the initial field work; that finding was substantiated by subsequent observations made in 1983, 1984, and 1992 during

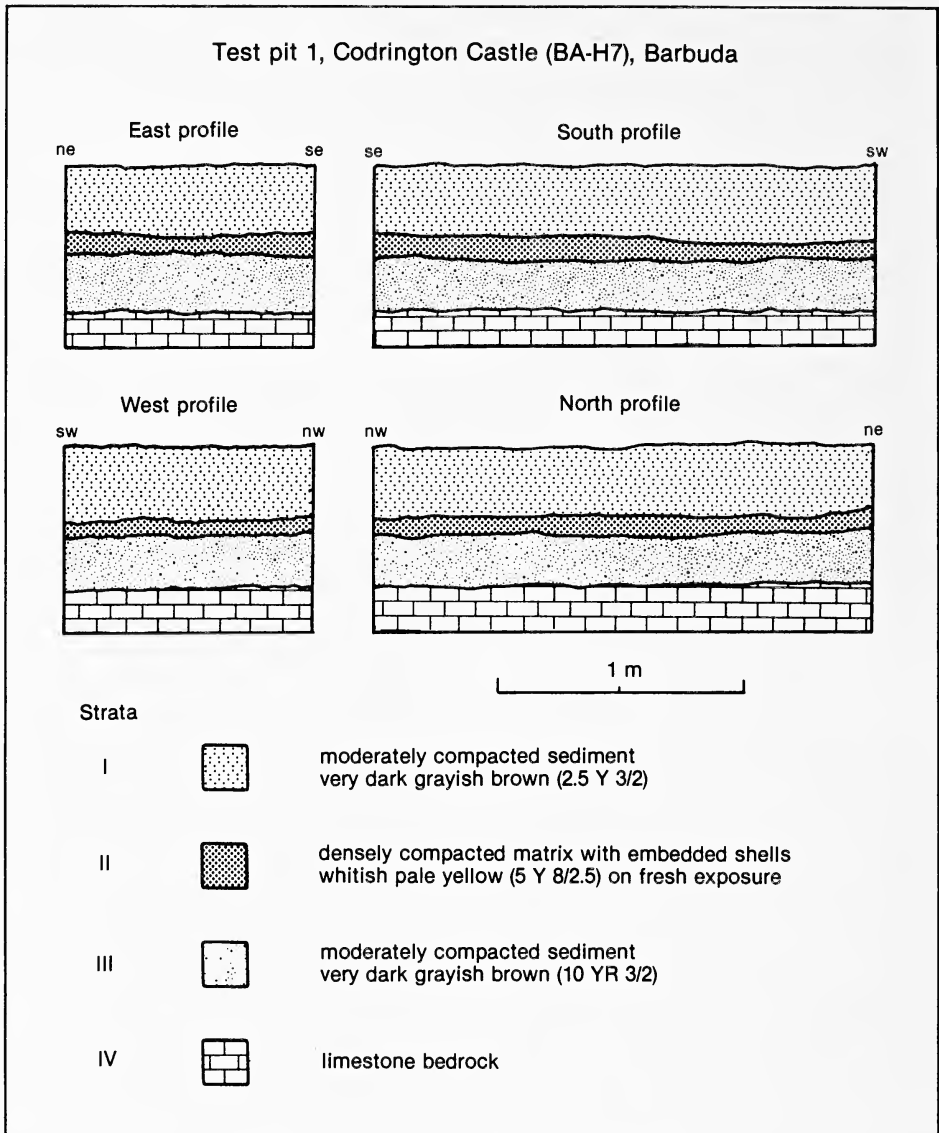


Fig. 12.—Stratigraphic profiles of test pit 1 at BA-H7.

other research projects on Barbuda. Castle Well and a few short lengths of aligned stones were the only surface indicators of Codrington Castle. According to Barbudan informants, the ginnery and cistern had been built with stones removed from the razed Castle.

The 1.0 × 2.0 m-test pit dug in April 1979 contained four strata (Fig. 12). Stratum I, a very dark grayish brown sediment (Munsell notations: dry 2.5 Y 3/2; wet 10 YR 3/1), was moderately compacted and reached depths of from 24 to 29 cm below ground surface; it was excavated in three 10-cm levels. Stratum II underlies Stratum I across the test pit. It was initially deemed (incorrectly) to be

bedrock because of its gray surficial color, hardness, and weathered appearance, all of which characterize the area's limestone. However, fresh surfaces of Stratum II, exposed when removed by a pick, showed a distinctive white to pale yellow color (5 Y 8/2.5) that differed from the gray color consistently seen on fresh surfaces of local limestone. Stratum II was determined to be a cultural layer, consisting of a purposefully spread and densely compacted "floor" (5–8 cm thick) with embedded small shells. Once removed, Stratum II was found to seal a second sediment layer, Stratum III. Stratum III was virtually identical to Stratum I, being moderately compacted and very dark grayish brown (dry 10 YR 3/2) to very dark brown (wet 10 YR 2/2) in color; it was 19–24 cm thick and was removed in two levels. Stratum III attained a maximum depth of about 58 cm below ground surface where it interfaced with Stratum IV, a layer of decomposing limestone pebbles grading into solid bedrock.

Test pit 1 included two artifact-bearing sediment deposits (Stratum I with levels 1–3 and Stratum III with levels 4–5) that were stratigraphically separated by the matrix comprising the cultural floor (Stratum II). Materials from the lowest part of Stratum I (Fig. 12), those items that were situated on the actual surface of the floor, were recovered and recorded separately in the field; in this paper, artifacts resting on the floor (none were actually embedded in the matrix) are tabulated as Stratum II (atop floor) materials, to distinguish them from level 3 artifacts. Three pieces of the consolidated matrix were obtained and designated Stratum II (floor samples). The deposits were dry-screened through 1/8-in mesh; cultural materials were segregated by stratum and level.

Material Culture Data Sets

Systematic archaeological research regarding the context and stratigraphy of cultural artifacts generates quantifiable data which provide the basis for determining the chronology and interpreting construction episodes of Codrington Castle. Such research provides otherwise unobtainable evidence of the Castle's extant subsurface remains, which augments the largely qualitative and descriptive information supplied by historical documentation.

Quantities of excavated artifacts from test pit 1 presented in this paper differ slightly from preliminary data provided previously (Watters, 1980b:138–140). These preliminary data were derived from field identifications made in 1979, following which most of the artifacts were left on the island in the care of the Barbuda Council. The test pit 1 collection was reexamined on Barbuda in May 1992; that analysis resulted in reclassification of certain artifacts and a slightly modified retabulation. The 1107 artifacts in test pit 1 include remnants of the building and glass, kaolin, metal, flint, and ceramic artifacts. Data for excavated specimens are tabulated separately for each artifact category in the following sections.

The excavated assemblage from 1979 is supplemented by 59 artifacts surface-collected at BA-H7 in May 1992. Data on the surface artifacts are compiled in Table 1 in order to distinguish them from excavated artifacts. However, certain of the surface-collected artifacts, especially glass and ceramics, will be used to augment subsequent discussion sections.

Structural Artifacts

Remnant components of the structure itself include plaster, slate, fired clay/brick, and mortar "floor" fragments (Table 2). Structural elements ($n = 557$) constitute 50.3% of total excavated artifacts.

Table 1.—*Surface-collected artifacts at Codrington Castle, Barbuda (May 1992).*

Material	Count	Remarks
Slate	1	
Glass	3	2 necks and finishes; 1 base
Ceramic		
Imported	6	Type 65 ($n = 1$), Type 54 ($n = 3$), Type 44 ($n = 2$)
West Indian	42	Afro-Caribbean
Category C	6	wheel-made, kiln-fired, unglazed
Kaolin pipe	1	stem bore diameter of 4/64 in
Total	59	

Plaster fragments (Fig. 13A–D), the most abundant structural artifact by count ($n = 484$) and weight (ca. 1.68 kg), are of a fairly uniform pink color (Munsell 5 YR 7/3) and most pieces have one flat side. The other side usually is rough with an uneven surface and sometimes includes remnants of a white mortar similar in color (5 Y 8/1), texture, and composition (including shell fragments) to the Stratum II floor material. This evidence indicates that the Castle's limestone walls first received an application of mortar to smooth out irregularities and perhaps to enhance adhesion, and then were coated with the pink plaster applied over the mortar. Alternatively, the white mortar and pink plaster may represent two temporally different episodes of wall treatment. The plaster was smoothed while still in its plastic state, thus creating the observed flat surface. There is a considerable range in plaster thickness (6.4–13.5 mm in a small sample measured), but thinner pieces definitely predominate. Plaster fragments were recovered above and below the Stratum II floor but they were far less abundant (5.1%) beneath it (Table 2).

Slate occurred only in the upper part of Stratum I, with 19 of 20 pieces being in the uppermost 10-cm level. The small (1–4 cm), thin (5 mm) pieces are shattered remnants of roofing slate broken when the Castle was being razed (Fig. 13E). Bits of adhering white mortar probably served to set the slate in place and seal its joints. One piece of slate was recovered on the surface in 1992 (Table 1).

The 50 fired clay lumps are amorphous, small (predominantly measuring about 1 cm but ranging upward), orange-red in color (sometimes overlain with a gray encrustation), and for the most part lack smooth surfaces. They seem to be interior remnants of larger objects, probably of bricks or clay tiles, although some could be lumps of daub. Their rough surfaces, composition, and texture distinguish the fired clay lumps from unglazed ceramic vessels. Clay lumps existed in all levels of the test pit, but they were minimally represented (6.0%) below the floor (Table 2).

The three floor samples recovered from the densely compacted matrix contain shell fragments and small mollusks (Fig. 13F). The matrix is a lime mortar or "cement" spread in its plastic state, creating a relatively level surface and concurrently sealing the strata beneath. This feature was purposefully set in place during a renovation at the Castle; its incidental sealing of underlying cultural deposits (Stratum III) was simply fortuitous. Embedded shells, including the Apple and West Indian murexes (*Phyllonotus pomum*, *Chicoreus brevifrons*), False Cerith (*Batillaria minima*), and Bubble-shell (*Bulla imbricata*), acted as binding agents helping to set the mortar. The samples definitely are not fossiliferous limestone containing naturally deposited mollusks. Stratum II was a cultural feature,

Table 2.—Excavated structural artifacts from Codrington Castle, Barbuda. Weight in gm.

Stratum/level	Slate			Plaster			Fired clay/brick			Mortar floor			Total	
	Count	% per level	Weight	Count	% per level	Weight	Count	% per level	Weight	Count	Weight	Count	Weight	Count
Stratum I														
1	19	95.0	39.1	9	1.9	44.1	6	12.0	37.2	—	—	—	34	120.4
2	1	5.0	0.5	45	9.3	138.9	19	38.0	34.7	—	—	—	65	174.1
3	—	—	—	370	76.4	1242.6	13	26.0	61.5	—	—	—	383	1304.1
Stratum II														
Atop floor	—	—	—	35	7.2	119.7	9	18.0	24.2	—	—	—	44	143.9
Floor matrix	—	—	—	—	—	—	—	—	—	3	929.5	—	3	929.5
Stratum III														
4	—	—	—	20	4.1	113.1	1	2.0	8.4	—	—	—	21	121.5
5	—	—	—	5	1.0	24.9	2	4.0	22.5	—	—	—	7	47.4
Total	20	100.0	39.6	484	99.9	1683.3	50	100.0	188.5	3	929.5	3	557	2840.9

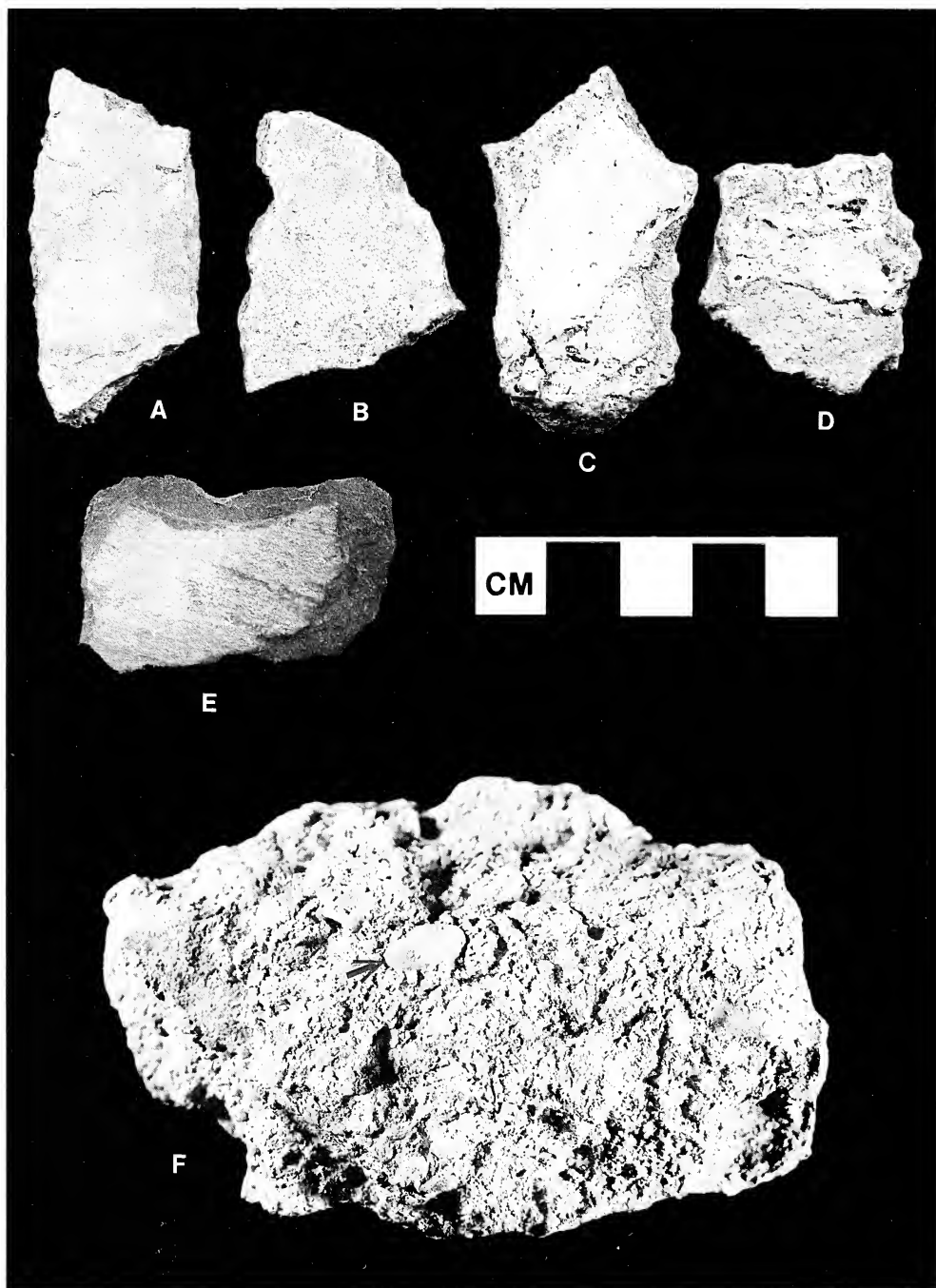


Fig. 13.—Structural artifacts. A–D, pink plaster fragments (note white mortar adhering to C and D); E, slate piece (FSN 375); F sample of floor mortar (arrow points to *Bulla imbricata* shell fragment).

forming a floor for a room within the Castle or a ground surface in the interior courtyard or the area surrounding the Castle (see discussion below).

Glass Artifacts

In Table 3, glass ($n = 273$) is tabulated primarily on the basis of color; it includes container ("bottle") and window glass, with the former being far more abundant.

The "patina/dark green" category includes the thick-bodied bottle glass fragments commonly found in British colonial period sites (Jones, 1986). They are the most abundant ($n = 144$) glass fragments, constituting 52.7% of total glass and having a cumulative weight of almost 1.2 kg. They range from darker green to almost black, are translucent to opaque, and usually contain bubbles. A patina resulting from chemical alteration is present on 116 specimens (80.6%). Although the vast majority of these fragments are body sherds having little diagnostic value, three excavated pieces retain finishes and necks (see below). Three bottle fragments were surface-collected in 1992 (Table 1).

The "clear/frosted/clouded" category incorporates the flat window glass, including pieces with patinated ("frosted") or iridescent ("clouded") surfaces, clear bottle glass (one modern piece has a design in yellow paint), and two articulating base fragments from a historic fluted tumbler (in Stratum III, level 4).

The remaining colored glass categories (yellow/brown, aqua, and light green) occur in the upper part of Stratum I (Table 3). The majority are translucent fragments of modern bottles, but a few pieces containing bubbles may be attributable to the historic period.

Table 3 shows that the patina/dark green glass sherds occur in all levels in the test pit; by count and percentage they are most abundant below the floor ($n = 82$; 56.9%). Their frequency ($n = 31$; 21.5%) immediately atop the floor equals the three upper levels in Stratum I. All other glass categories are restricted to the uppermost part (level 1), except for one aqua (level 2) and three clear (level 4) fragments, and while level 1 has the greatest abundance of glass ($n = 138$), its specimens are mostly modern. The absence of modern glass elsewhere in test pit 1 indicates the undisturbed (by recent intrusion) context of the cultural deposits below level 1.

Six broken bottles (five necks and finishes and one heel and base) retain sufficient diagnostic attributes to enable their chronological placement. All belong to the dark green/patina category, with three being excavated (Table 3) and three surface-collected (Table 1); two excavated bottles (Fig. 14A, B) show heavy patination. Table 4 provides provenience, descriptive, and metrical data for the five bottles with finishes and necks; lip and string rim attributes in particular are variable. Analytical methodology and terminology follow Jones (1986, 1989), who also kindly advised on dates of the bottles.

Finishes and necks on three longitudinally split bottles retain approximately one-half of their bores in two cases (FSN 157 and 373) and one-third in one case (FSN 372). Two bottles (FSN 216 and 217) have full finishes and bores and also retain sizable portions of their necks.

Two bottles from level 4, FSN 217 and 216 (Fig. 15A, B), the only datable bottle fragments found beneath Stratum II, are dated, respectively, to ca. 1730–1785 and the mid-18th century. These two contemporaneous bottles reveal dramatically different degrees of patination (Fig. 14A, C). The third bottle, FSN 157

Table 3.—Excavated glass artifacts from Codrington Castle, Barbuda. Weight in gm.

Stratum/level	Patina/dark green			Clear/frosted/clouded			Yellow/brown			Aqua			Light green			Total	
	Count	% per level	Weight	Count	% per level	Weight	Count	% per level	Weight	Count	% per level	Weight	Count	% per level	Weight	Count	Weight
Stratum I																	
1	13	9.0	40.8	72	96.0	182.4	15	100.0	13.8	6	85.7	15.8	32	100.0	63.9	138	316.7
2	13	9.0	53.8	—	—	—	—	—	—	1	14.3	0.5	—	—	—	14	54.3
3	5	3.5	21.3	—	—	—	—	—	—	—	—	—	—	—	—	5	21.3
Stratum II																	
Atop floor	31	21.5	323.4	—	—	—	—	—	—	—	—	—	—	—	—	31	323.4
Stratum III																	
4	49	34.0	342.1	3	4.0	33.0	—	—	—	—	—	—	—	—	—	52	375.1
5	33	22.9	418.3	—	—	—	—	—	—	—	—	—	—	—	—	33	418.3
Total	144	99.9	1199.7	75	100.0	215.4	15	100.0	13.8	7	100.0	16.3	32	100.0	63.9	273	1509.1

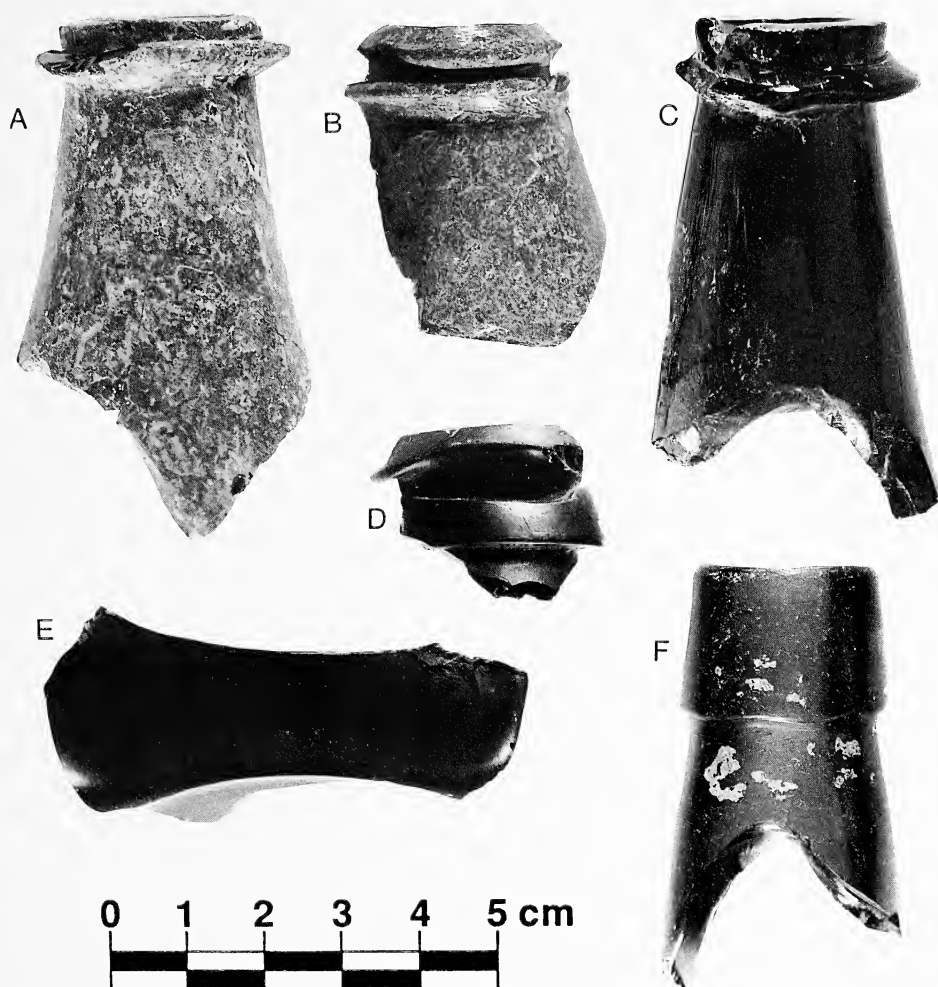


Fig. 14.—Bottle glass from Codrington Castle. A, FSN 217, level 4; B, FSN 157, atop floor; C, FSN 216, level 4; D, FSN 372, surface; E, FSN 374, surface; F, FSN 373, surface. Note the patination on A and B.

(Fig. 14B, 15D), excavated from immediately atop the floor, is well patinated although it dates more recently, between ca. 1790 and 1820. A fourth bottle fragment, FSN 372 (Fig. 14D; 15E, F), was a surface find which dates to about 1760–1780. The fifth bottle, FSN 373 (Fig. 14F, 15C), the only one having a one-part finish, dates to the second half of the 19th century. The sixth bottle fragment (Fig. 14E), of which about one-quarter remains, consists of a very slightly bulged heel, an arched (shallow concave) base, and one complete and two partial resting points (a corresponding fourth point is missing). This fragment is a case bottle base.

Kaolin Smoking Pipes

The sample of kaolin smoking pipes includes 14 excavated fragments (Table 5) and one surface-collected stem (Table 1). An intact bowl (Fig. 16A) from level

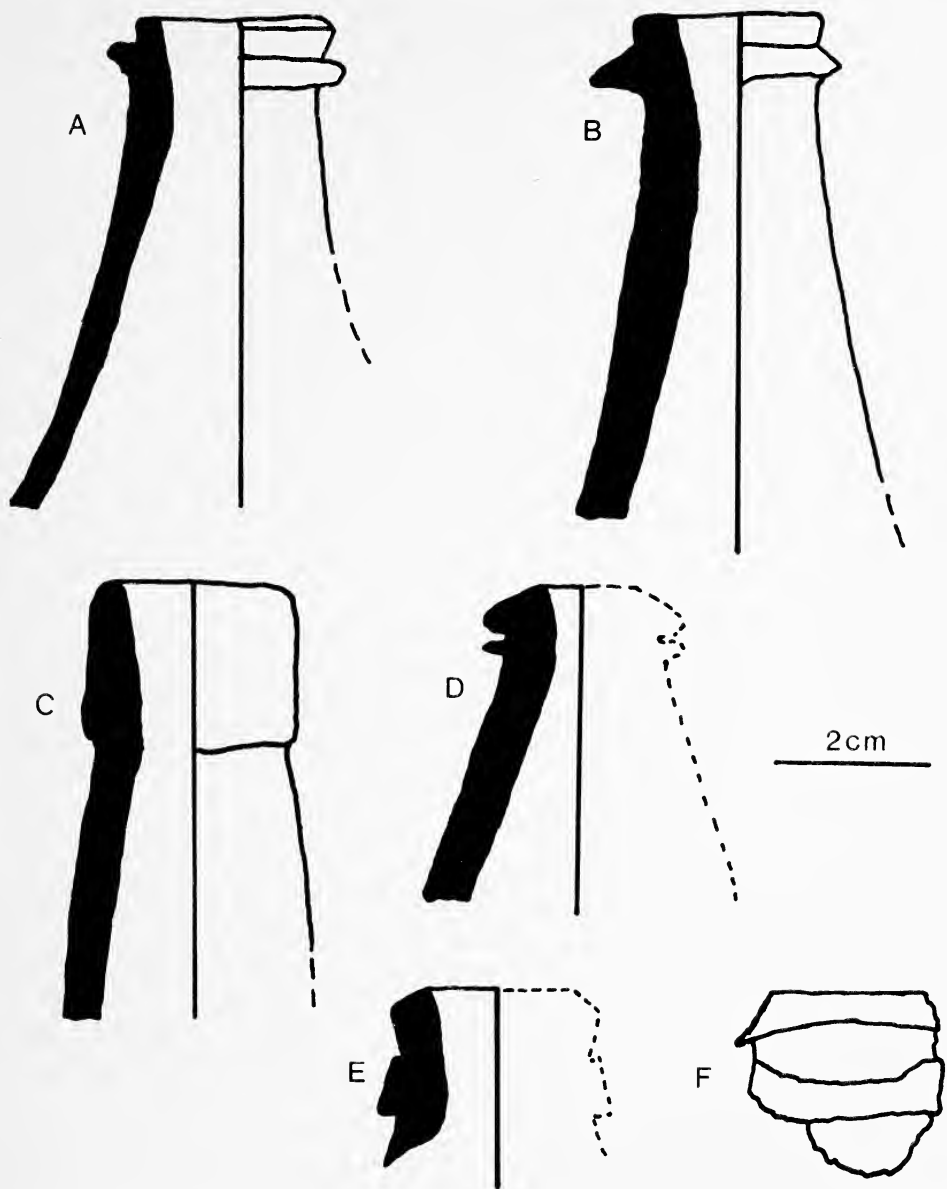


Fig. 15.—Profiles of the glass bottles. A, FSN 217; B, FSN 216; C, FSN 373; D, FSN 157; E, FSN 372; F, depiction of the highly variable height between the bottom of the lip and top of the string rim of FSN 372.

5, the deepest part of the test pit, has a heel spur and a bulbous bowl that angles out from the stem; it closely resembles a pipe illustrated by Noël Hume (1969: fig. 97, pipe 11) and dated from 1645 to 1665. The intact bowl and two bowl fragments have charred interiors; two other bowl fragments are blackened on their interiors and exteriors. Stems of varying lengths predominate ($n = 9$) among

Table 5.—*Excavated kaolin smoking pipe artifacts from Codrington Castle, Barbuda. Weight in gm.*

Stratum/level	Bowl		Stem		Total		Bore diameter distribution (in)		
	Count	Weight	Count	Weight	Count	Weight	4/64	5/64	6/64
Stratum I									
1	—	—	1	1.6	1	1.6	—	1	—
2	—	—	2	3.4	2	3.4	1	1	—
3	—	—	—	—	—	—	—	—	—
Stratum II									
Atop floor	2	0.7	3	5.9	5	6.6	—	—	3
Stratum III									
4	2	1.5	2	5.7	4	7.2	—	1	1
5	1	11.9	1	1.8	2	13.7	—	1	1 ^a
Total	5	14.1	9	18.4	14	32.5	1	4	5

^a Shank of bowl.

excavated fragments (Fig. 16F–O). The tip of one stem was intentionally ground until smooth (Fig. 16H). The pipes display neither makers' marks nor decoration.

Bore diameters, measured for nine excavated stems and at the intact bowl's shank, are presented in their stratigraphic context in Table 5. The larger bores (6/64 and 5/64 in), prevalent from the last decades of the 17th century through the first half of the 18th century, occur below and above Stratum II; a stem with the smallest bore diameter (4/64 in), which predominates after about 1750, was recovered exclusively above the floor (cf. Noël Hume, 1969:fig. 96).

Metal Artifacts

Metal artifacts were abundant but poorly preserved, and the iron artifacts in particular, which already had been rusted badly when excavated, further corroded while stored on Barbuda. Thus, 138 metal fragments initially recovered in 1979 had broken down into 182 fragments by 1992. Table 6 is the 1992 tabulation.

"Flat pieces" ($n = 99$) are most abundant and comprise 54% of total metal artifacts. A functional classification of the pieces is not feasible as they are thin, small, and rusted fragments of larger objects. Iron nails and fragments are next most abundant ($n = 78$; 43%). There is considerable range in nail size, or so it appeared despite their fragmentary condition. Some nails likely were used in building Codrington Castle and thus could be regarded as structural artifacts. In this study all nails are aggregated in the metal artifacts sample, because there is no effective way to distinguish nails used in building construction from nails used for other purposes. Other metal artifacts are limited to a hacksaw blade, screw, piece of wire, and two lead lumps (from levels 1 and 3).

Flat pieces and nails, the only metal artifact categories present in all levels of test pit 1, occur with greater frequency above the floor (Table 6). Metal artifacts are most abundant ($n = 85$; 47%) in level 1, the uppermost part of the test pit. Three artifacts that can be characterized as probably modern hardware—the hacksaw blade, screw, and perhaps the wire piece—came from level 1.

Flint/Chert Artifacts

These ten excavated artifacts pose interesting issues of interpretation. They are presumed to have been used during the colonial era since they are provenienced

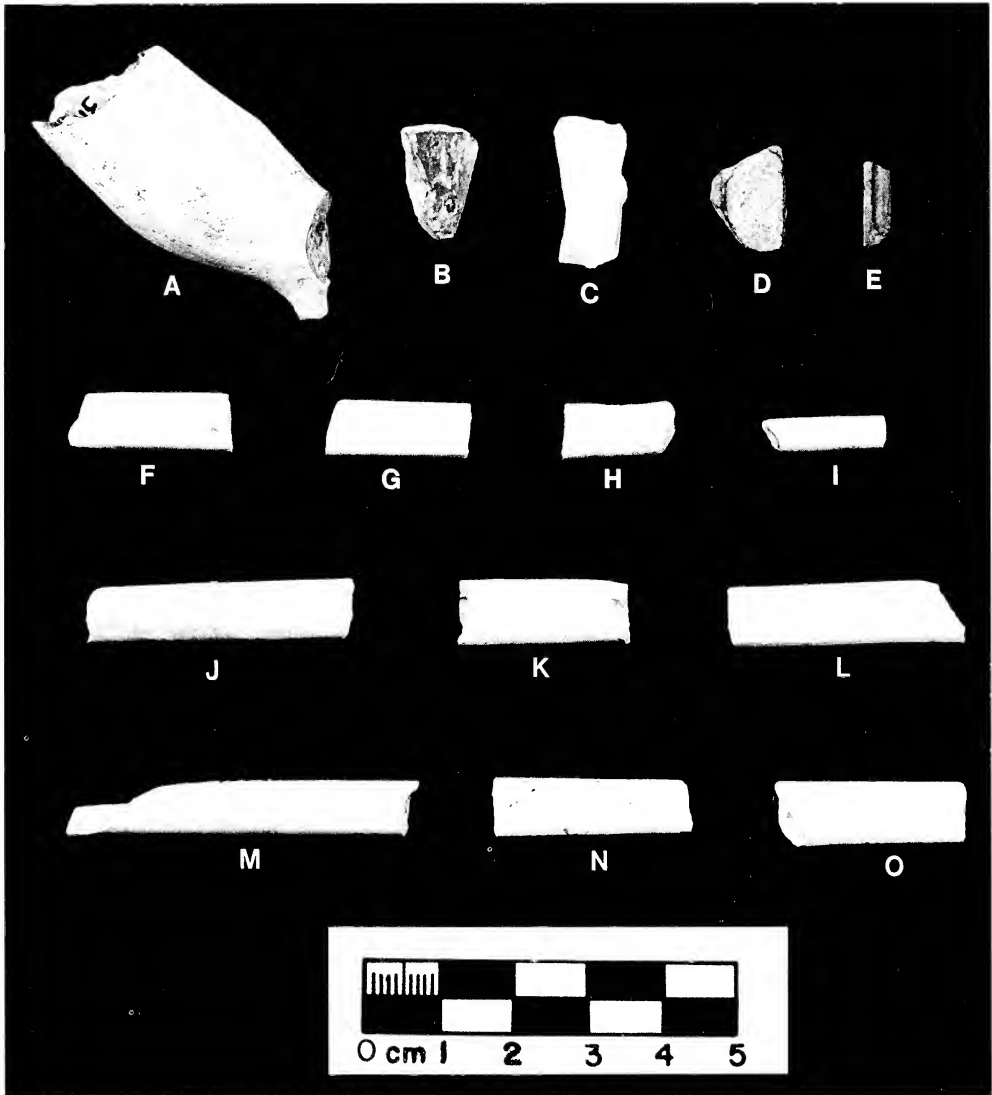


Fig. 16.—Kaolin smoking pipe fragments from Codrington Castle. A, intact bowl (FSN 313); B–E, bowl fragments (FSN 228, 227, 183a, 183b); F–O, pipe stems (FSN 312, 42, 166, 88, 164, 226, 87, 225, 165, 371). All were excavated except O (1992 surface collection); H has a ground tip; bore diameters correlated with specimens include 6/64 in (A at shank, H, J, K, N), 5/64 in (F, G, L, M), and 4/64 in (I).

to a historic site, and one artifact, a gunflint (Fig. 17A), undoubtedly is a historic object. However, the other nine artifacts (classed as nodules, cores, flakes, and shatter; Table 7) have generic attributes that occur in a wide range of cultural contexts and temporal periods. These nine artifacts have neither form nor function attributes that can be deemed distinctive to the historic period, although one piece (FSN 300) shows a spalled edge that possibly resulted from its use as a strike-a-light (flint fire-starter). Some specimens, were they to be placed in a lithic

Table 6.—Excavated metal artifacts from Codrington Castle, Barbuda. Weight in gm.

Stratum/level	Flat pieces		Nail fragments		Lead lumps		Hacksaw blade		Screw		Wire		Total ^a	
	Count	Weight	Count	Weight	Count	Weight	Count	Weight	Count	Weight	Count	Weight	Count	Weight
Stratum I														
1	59	102.7	22	127.7	1	3.9	1	3.3	1	2.1	1	2.2	85	241.9
2	18	41.4	14	115.1	—	—	—	—	—	—	—	—	32	156.5
3	3	27.4	14	36.4	1	18.4	—	—	—	—	—	—	18	82.2
Stratum II														
Atop floor	15	35.9	16	56.6	—	—	—	—	—	—	—	—	31	92.5
Stratum III														
4	3	5.3	8	16.2	—	—	—	—	—	—	—	—	11	21.5
5	1	26.1	4	6.6	—	—	—	—	—	—	—	—	5	32.7
Total	99	238.8	78	358.6	2	22.3	1	3.3	1	2.1	1	2.2	182	627.3

^a Excludes weights of bits of "scrap" in each level; total scrap weight is 34.6 gm.

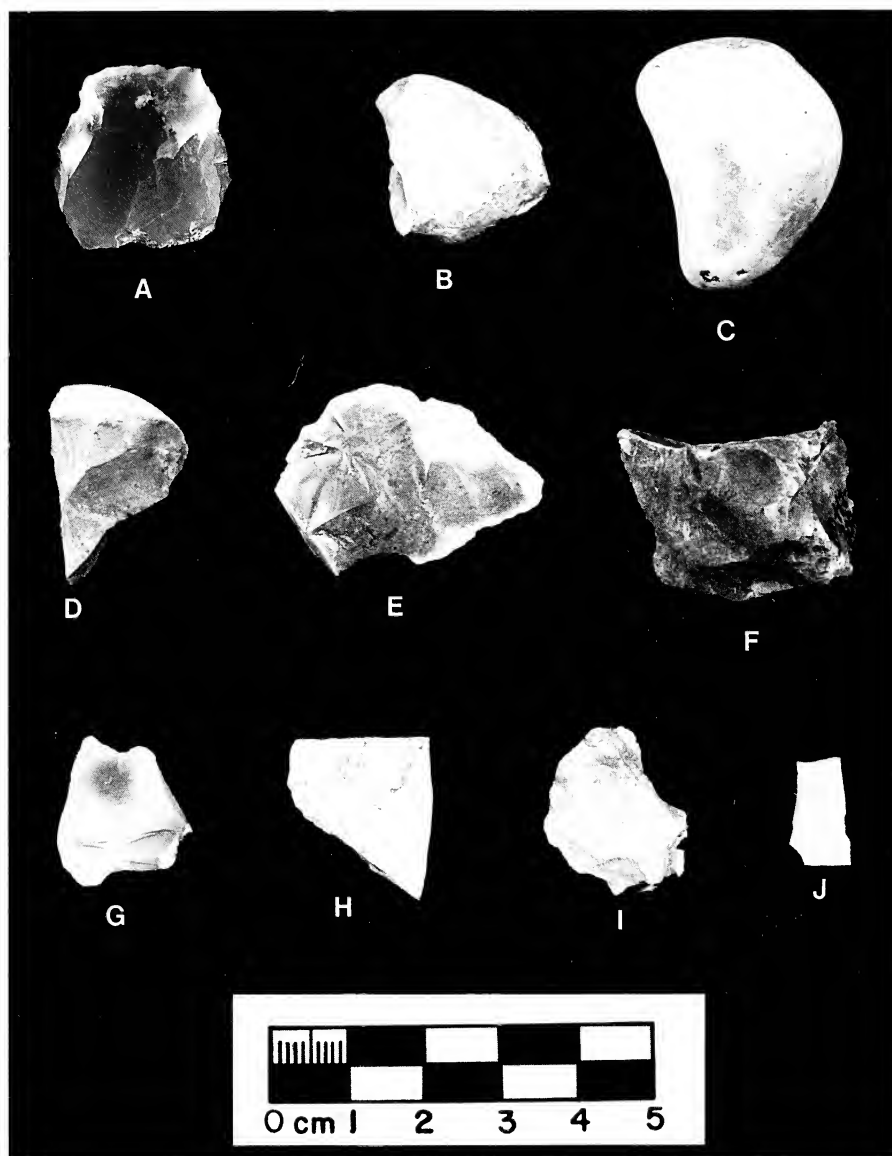


Fig. 17.—The flint/chert artifacts excavated at Codrington Castle. A, French gunflint (FSN 156); B, core fragment (FSN 73); C, nodule (FSN 213); D, core fragment (FSN 71); E, flake (FSN 215); F, core (FSN 300); G, flake (FSN 72); H, shatter (FSN 301); I, shatter (FSN 113); J, flake (FSN 74). E, G, and J are attributed to chert sources on Antigua; D and F probably are from Antigua.

assemblage from a Lesser Antilles Amerindian site, would be indistinguishable from the prehistoric artifacts.

The dual “flint/chert” designation reflects a multitude of issues regarding the variable use of these terms by geologists and archaeologists (see discussion in Hamilton and Emery, 1988:5–9). As used here, “flint” implies that Europe was the source of the raw materials, while “chert” implies a West Indian geological

Table 7.—*Excavated flint/chert artifacts from Codrington Castle, Barbuda. Weight in gm.*

Stratum/level	Nodule		Core		Flake		Shatter		Gunflint		Total	
	Count	Weight	Count	Weight	Count	Weight	Count	Weight	Count	Weight	Count	Weight
Stratum I												
1	—	—	—	—	—	—	—	—	—	—	—	—
2	—	—	2	11.7	2	1.2	—	—	—	—	4	12.9
3	—	—	—	—	—	—	1	2.8	—	—	1	2.8
Stratum II												
Atop floor	—	—	—	—	—	—	—	—	1	4.4	1	4.4
Stratum III												
4	1	23.6	1	14.9	1	5.1	—	—	—	—	3	43.6
5	—	—	—	—	—	—	1	2.1	—	—	1	2.1
Total	1	23.6	3	26.6	3	6.3	2	4.9	1	4.4	10	65.8

source. Lithic artifacts found at a historic site in the West Indies potentially could originate from European flint sources. However, such lithics also potentially could have come from chert geological deposits within the West Indies, including the same sources previously exploited by Amerindians. In fact, Amerindian sites themselves potentially were sources of chert to be “mined” by the later European and African inhabitants of these islands.

Antigua is the only northern Lesser Antilles island having geologically documented chert deposits. Martin-Kaye (1959:11) terms these deposits the Corbison Chert Beds; Weiss (1994:17) indicates they are cherty biostromes. The best known geologic deposit, which was exploited extensively during the prehistoric era, is Flinty Bay on Long Island, a small island off Antigua's northeast coast. Two chert deposits, Little Cove and Corbison Point, are known from Antigua proper, and other sources as yet undiscovered likely exist (Watters and Donahue, 1990). Although Antigua has the only documented geologic deposits, chert may be more widely distributed in the Leeward Islands. Walker (1980:61–65) attributes to St. Kitts itself the chert pebbles (his flint types 1 and 2) he found among beach gravels on that island; his Type 3 is attributed to Flinty Bay, Antigua. Chert has not been identified in Barbuda's geologic formations. Whereas in the past archaeologists have had to assume that Antigua's deposits were the primary sources for chert nodules, artifacts, and debitage recovered at prehistoric sites throughout the northern Lesser Antilles, there is now a program of laboratory analyses to test the Antigua source hypothesis and to distinguish the geochemical signatures for Antigua cherts, the preliminary results of which are promising (Knippenberg, 1995).

Archaeologists who are familiar with Antiguan chert from prehistoric sites have examined the Codrington Castle lithics, and they concur with the author's assessment that some of these specimens have strikingly similar characteristics. Three flakes (Fig. 17E, G, J) are ascribed to Antiguan chert sources on the basis of macroscopic and microscopic examinations. A primary flake, FSN 215, has a light yellow-brown (10 YR 8/3), relatively thick (4.5 mm) calcareous cortex covering the entire surface of one side. The flake's opaque core is very dark gray (5 Y 3/1) with a slightly olive cast; its color changes to light yellowish brown (10 YR 6/4) along fracture planes and at the boundary of the core and cortex, where it thins to translucency. A second flake, FSN 72, retains no cortex; the third (FSN 74) has a tiny amount. Both flakes are translucent near their thinned edges and

possess identical core colors, varying in each flake from pale olive (5 Y 6/3) to light yellowish brown (2.5 Y 6/4). FSN 74 also exhibits a small black (5 YR 2.5/1) spot encircled by a halo of dark reddish brown (5 YR 3/2) (Fig. 17G). These three flakes compare well with the first variety of Walker's (1980:64–65) Type 3 black-and-tan Antigua flint. The author has observed similar black-inclusion chert in prehistoric artifacts (on Antigua and other islands) that are presumed to be from Antiguan sources.

The core color, dark olive-gray (5 Y 3/2), is identical in two other Codrington Castle lithics, a core (FSN 300) and a core fragment (FSN 71), and the color is similar to the FSN 215 flake; all three have a glossy luster. The visible cortex on the core fragment is darker, smoother, and much thinner (<0.5 mm) than the flake's cortex. The core and core fragment (Fig. 17D, F) are referred provisionally to Antiguan chert sources.

The four remaining lithic specimens do not correlate with Antiguan cherts known to the author. The two shatter fragments (Fig. 17H, I) are pink (5 YR 7/4) to light reddish brown (5 YR 6/4) and exhibit pot-lid fractures from thermal alteration. FSN 301 retains a thin (<0.5 mm) cortex mottled in yellow (10 YR 7/4) and gray (5 Y 6/1) on one side. A core fragment (FSN 73), comprised of slightly less than half of a pebble (Fig. 17B), has an olive interior (5 Y 5/3) and yellow (10 YR 8/8) cortex about 1.5 mm thick. Thinly distributed over the cortex are patches of dark red (2.5 YR 3/6) and gray (2.5 Y 6/0). The ninth specimen, a small nodule (Fig. 17C) with a maximum dimension of 33.12 mm, exhibits a light yellow-brown (10 YR 6/4) cortex with strong brown (7.5 YR 5/6) patches. Core color cannot be determined for this intact nodule.

The Antiguan origin attributed to three (perhaps five) of these specimens is the first instance in which Antiguan chert has been reported from a historic site on Barbuda. Nonetheless, the process by which these artifacts came to be incorporated within the cultural deposits at Codrington Castle remains uncertain. Direct exploitation of Antigua's chert deposits by Europeans or Africans during the colonial era, followed by shipment of these materials to Barbuda, is one feasible process. Equally plausible, however, is historic period reuse of Antiguan chert nodules or artifacts mined from prehistoric sites on Barbuda, all of which are known to contain such lithic materials (Watters, 1980a:tables 13–16). One flake (Fig. 17E) is a particularly good candidate for being a "recycled" prehistoric artifact.

The gunflint (Fig. 17A), found atop the floor (Stratum II) in the Codrington Castle test pit, was examined and commented on by Barry Kent (personal communication, 1994), an expert on gunflints. This specimen (FSN 156) possesses the "honey color," translucency, and high sheen that are characteristic of French flint. The white sectors visible in the artifact result from geologic inclusions in the rock rather than use wear. The gunflint was made on a prismatic blade, exhibits three blade scars or facets, and has a blunted or rounded heel (Fig. 18). Examination of its edge wear indicates this flint is well used but not exhausted. Such a gunflint would have been appropriate in a fowler, rifle, or large pistol lock. With a heel-to-edge maximum dimension of 23.68 mm, it is too small for a musket flint.

French blade flints made their first appearance by at least 1650, but the form attained its greatest popularity in the second half of the 18th century and its production continued well into the 19th century. In view of the long production span of French blade flints, more precise dating of a single gunflint is not feasible.

BA-H7-156

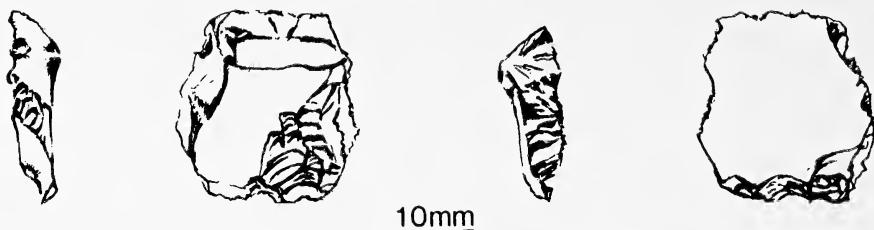


Fig. 18.—Details of edge wear on the French gunflint.

However, this manufacturing span is in accord with most of the occupation span at Codrington Castle. From the stratigraphic standpoint, an association between the gunflint and a French attack on the Castle in 1710 is impossible because the gunflint was recovered atop the floor which was constructed subsequent to that assault. The presence of a French gunflint at a British site is not unusual because French flint was preferred, due to its superior quality, throughout the colonial period (Noël Hume, 1969:220).

Ceramic Artifacts

There is considerable diversity in the ceramic artifacts recovered at Codrington Castle. Technological attributes used to categorize these sherds are: (1) method of manufacture, either wheel-made or hand-built (coiled); (2) method of firing, either kiln-fired or open hearth-fired; and (3) application of a glaze. Most wheel-made, kiln-fired, and glazed sherds are European export ceramics. On the other end of the spectrum are coil-built, hearth-fired, and unglazed sherds, probably all of which were made in the West Indies. Between these extremes are three nebulous categories comprised of predominantly wheel-made and kiln-fired ceramics, both glazed and unglazed, the origins of which are unclear. The sample of 71 excavated ceramics is augmented by 54 more sherds surface-collected in the vicinity of the site in May 1992 (Table 1).

Imported Ceramics.—Of 71 sherds from test pit 1 (Table 8), imported ceramics account for 64.8%. These 46 sherds, all of which are wheel-made, kiln-fired, and glazed, were exported to the West Indies from European production centers (except for two Chinese porcelain pieces). They include earthenware ($n = 30$), stoneware ($n = 6$), porcelain ($n = 2$), and “Unclassed” ($n = 8$) sherds (Table 9). Twenty-nine sherds (63.0%) can be ascribed to 12 of South’s (1977:table 31) ceramic types; nine others cannot be typed but are classifiable as earthenwares or stonewares.

Of the 12 types, the eight earthenwares include creamware (Type 22; hereafter T22), pearlware (T19 and T20), slipware (T56), refined (T2 and T33), and tin-enamelled (T49 and T56) sherds, totaling 25 artifacts (Table 9). Untyped earthenware sherds ($n = 5$) include one Staffordshire-like mottle-glaze mug fragment, a lead-glazed redware bowl rim (probably French in origin), and three fragments of delft paste from which the tin-enamelled glaze has separated.

Typed stonewares are White salt-glazed (T40) and British brown stoneware (T54); untyped stoneware specimens include three brown-surfaced, gray-bodied pieces and one Rhenish gray stoneware fragment. Typed Chinese porcelains in-

Table 8.—*Excavated ceramic artifacts from Codrington Castle, Barbuda. Weight in gm.*

Stratum/level	Imported			West Indian			Category A			Category B			Category C			Total		
	Count	% per level	Weight	Count	% per level	Weight	Count	% per level	Weight	Count	% per level	Weight	Count	% per level	Weight	Count	% per level	Weight
Stratum I																		
1	11	23.9	18.9	4	44.4	18.0	1	16.7	1.0	2	25.0	2.7	—	—	—	18	25.4	40.6
2	11	23.9	12.2	1	11.1	11.4	2	33.3	5.4	—	—	—	—	—	—	14	19.7	29.0
3	3	6.5	18.7	1	11.1	23.0	—	—	—	—	—	—	—	—	—	4	5.6	41.7
Stratum II																		
Atop floor	11	23.9	27.3	3	33.3	16.4	1	16.7	9.3	2	25.0	13.4	—	—	—	17	23.9	66.4
Stratum III																		
4	6	13.0	8.6	—	—	—	2	33.3	5.3	4	50.0	70.7	2	100.0	12.7	14	19.7	97.3
5	4	8.7	18.1	—	—	—	—	—	—	—	—	—	—	—	—	4	5.6	18.1
Total	46	99.9	103.8	9	99.9	68.8	6	100.0	21.0	8	100.0	86.8	2	100.0	12.7	71	99.9	293.1

Table 9.—Stratigraphic distribution of excavated imported ceramics from Codrington Castle, Barbuda.

Type number or class ^a	Stratum I			Stratum II Atop floor	Stratum III		Total per type	
	1	2	3		4	5	Count	%
Earthenware								
2 whiteware	1	—	—	—	—	—	1	2.2
20 undecorated pearlware	1	1	—	—	—	—	2	4.3
19 blue-edged pearlware	2	2	—	—	—	—	4	8.7
22 creamware	2	1	—	—	—	—	3	6.5
33 green-glazed cream-bodied ware	—	1	—	—	—	—	1	2.2
65 plain white delftware	—	—	—	3	3	1	7	15.2
49 18th century decorated delftware	—	—	—	2	—	2	4	8.7
56 lead-glazed slipware	—	—	—	3	—	—	3	6.5
— Staffordshire-like mottle-glaze slipware	—	1	—	—	—	—	1	2.2
— lead-glazed redware (French?)	—	—	—	1	—	—	1	2.2
— delftware paste	—	—	—	—	3	—	3	6.5
Earthenware total	6	6	0	9	6	3	30	65.2
Stoneware								
40 white salt-glazed	1	—	—	—	—	—	1	2.2
54 British brown	—	—	—	—	—	1	1	2.2
— brown-surfaced, gray-bodied	—	—	3	—	—	—	3	6.5
— Rhenish gray	—	—	—	1	—	—	1	2.2
Stoneware total	1	0	3	1	0	1	6	13.1
Porcelain								
39 underglaze blue	—	1	—	—	—	—	1	2.2
26 overglaze enamelled export	—	—	—	1	—	—	1	2.2
Porcelain total	0	1	0	1	0	0	2	4.4
Unclassed	4	4	—	—	—	—	8	17.3
Total count per level	11	11	3	11	6	4	46	
%	23.9	23.9	6.5	23.9	13.1	8.7		100.0

^a Type number after South (1977:table 31).

clude Underglaze blue (T39) and Overglazed enamelled export (T26) sherds. Eight "Unclassed" sherds are unable to be further distinguished because their size is too small or their surfaces have eroded too much for confident assignment. Figure 19 illustrates various imported ceramics.

Table 10 shows the manufacturing date ranges and median dates of the 12 typed ceramics. All types were manufactured during the 18th century except for the single whiteware (T2) sherd. Median dates for nine types are of the 18th century, and two dates are earliest 19th century (1805). By using South's (1977:chapter 7) Mean Ceramic Date Formula, the 29 typed sherds yield a Mean Date of 1759; if T65 is excluded (see Table 10), the remaining 22 sherds provide a date of 1772—a disparity of 13 years.

The stratigraphic contexts of excavated earthenware sherds generally are in proper temporal relationship. Types having more recent median dates, such as whiteware, pearlware, and creamware, are restricted to the two upper levels, whereas those with older median dates, delftware and lead-glazed slipware, occur only atop the floor and in levels 4 and 5 beneath it.

Six typed sherds from the surface include an undecorated delft earthenware

(T65), three conjoining British brown stoneware (T54), and two conjoining Westerwald gray stoneware (T44) sherds (Table 1). The Westerwald pieces contain cobalt-blue splotches and a zoomorphic embellishment incorporating the tail, back legs, and body (the head is missing) of a lion-like figure (Fig. 19J).

West Indian Ceramics.—All nine coil-built, hearth-fired, and unglazed sherds (Fig. 20) in test pit 1 were excavated from Stratum I, with six being in levels 1–3 and three immediately atop the floor (Table 8). In 1992, 42 sherds (Table 1) having those same attributes were collected from the surface of the BA-H7 site and a historic dump near the mangroves (Fig. 11). The excavated and surface sherds from Codrington Castle augment an expanding sample of Afro-Caribbean ceramics being analyzed from Barbuda, Antigua, Montserrat, and Anguilla (Petersen and Watters, 1988; Petersen et al., 1992). “Afro-Caribbean” currently is the broadest term used in the English-speaking Caribbean to encompass such pottery, although “folk pottery” and even “Colono Ware,” a North American-derived term, have been applied in the West Indies (Watters, 1980*b*, 1987; Heath, 1988; Nicholson, 1990). Island-specific designations such as Afro-Montserratian, Afro-Antiguan, Afro-Jamaican, and Afro-Cruzan also appear in the literature (see Petersen and Watters, 1988:168). It is improper to characterize all Afro-Caribbean pottery as “slave-made” since it was made both before and after emancipation; and furthermore, even during the slavery period, freed blacks may have produced some of the Afro-Caribbean pottery.

The term “Afro-Caribbean” implies that the pottery was made in the West Indies by Africans or their descendants. However, an even more significant point is that these unglazed ceramics were made in the African *tradition* of coil-built, open-hearth fired manufacture (Petersen and Watters, 1988). These ceramics were made in the West Indies by potters using a technology derived from Africa; by extension, the potters presumably were of African heritage. The West Indian ceramics made in the African tradition contrast with the West Indian wheel-made and kiln-fired ceramics derived from the European pottery-making tradition (see following section).

Fifty-one sherds have been assigned to the Afro-Caribbean ceramic category pending the completion of a detailed vessel-lot attribute analysis (see Petersen and Watters, 1988). Petersen’s provisional analysis indicates these sherds can be confirmed (or reasonably inferred in a few cases) to be coil built, open-hearth fired, and unglazed. The collection contains examples of thinner 18th- and 19th-century Afro-Caribbean sherds (Fig. 20A, B, D, E) as well as the generally thicker post-emancipation pottery, the production of which persisted well into the 20th century, most notably at Sea View Farm, Antigua (Fig. 21).

The excavated sherds generally are smaller than the surface-collected ceramics. Excavated rims (Fig. 20A, E) have gray (10 YR 5/1) and reddish yellow (7.5 YR 6/6) exteriors. Two body sherds (Fig. 20B, D) are dark gray (2.5 YR 4/0) and dark reddish gray (5 YR 4/2) respectively. Interior and exterior surfaces of one reddish yellow (5 YR 6/6) body sherd are burnished (Fig. 20F). The smallest excavated body sherd (Fig. 20G) is reddish yellow (7.5 YR 6/6) on both its exterior and interior surfaces; it is the only slipped sherd and retains remnants of a reddish brown (2.5 YR 5/4) slip. One body sherd is grayish brown (10 YR 5/2) on both surfaces (Fig. 20C). Two body sherds (Fig. 20H, I) from levels 2 and 3 conjoin and have grayish brown (10 YR 5/2) exteriors with red (2.4 YR 4/6) interiors.

At least 16 surface-collected sherds retain slips, usually red (2.5 YR 5/6) but

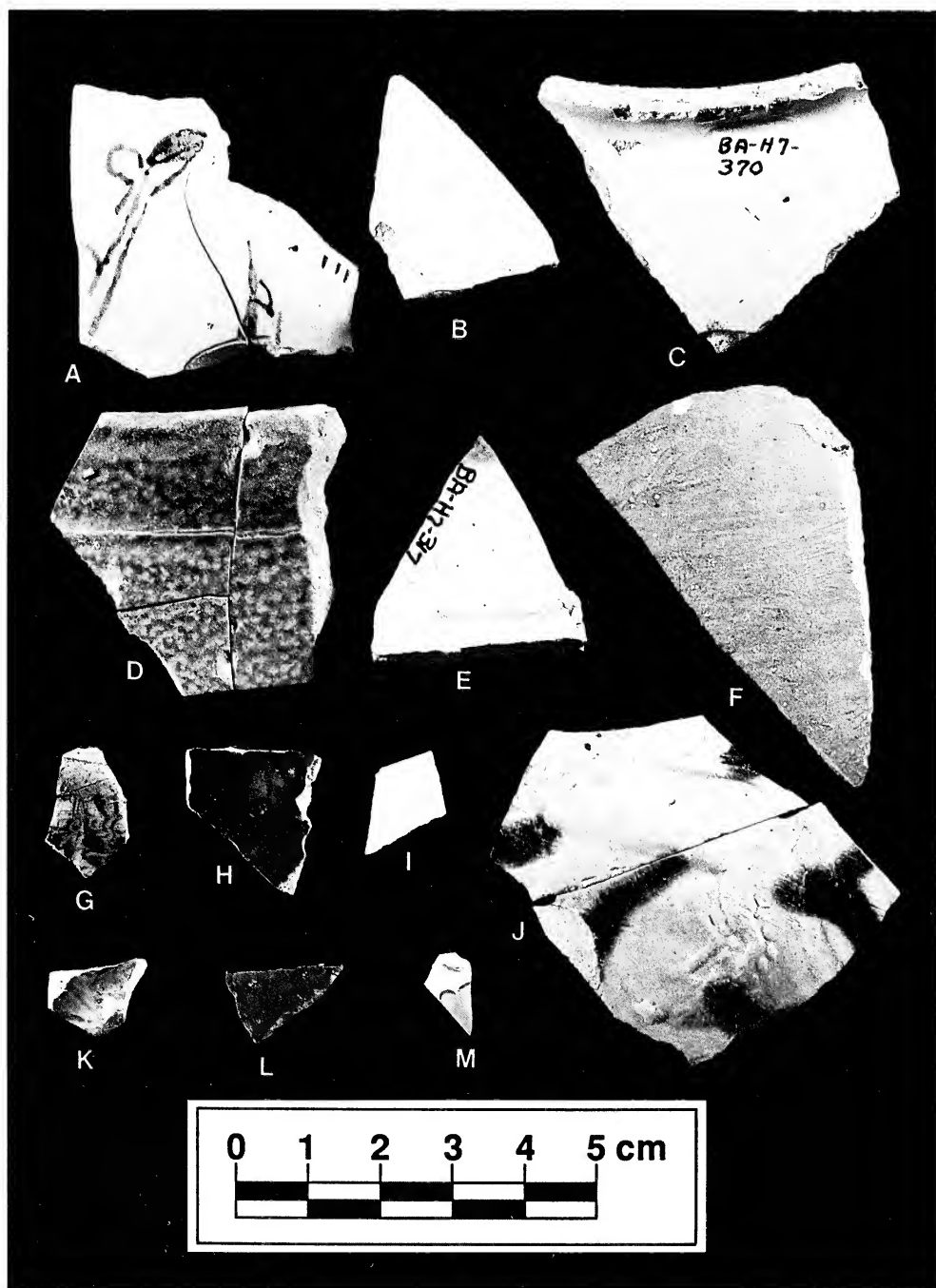


Fig. 19.—Imported ceramics. A, decorated delftware (Type 49), level 5 (FSN 314 and 315); B, plain white delftware (T65), level 5 (FSN 316); C, plain white delftware (T65), surface (FSN 370); D, gray-bodied British brown stoneware (T54), surface (FSN 368, 369a, and 369b); E, white-bodied British brown stoneware (T54), level 5 (FSN 317); F, untyped gray-bodied brown stoneware, level 3 (FSN 123); G, lead-glazed slipware (T56), atop floor (FSN 174); H, untyped Staffordshire-like mottle-glaze earthenware, level 2 (FSN 96); I, untyped Rhenish gray stoneware, atop floor (FSN 178); J, Westerwald

also tending toward a more reddish brown hue (5 YR 5/4). The amount of extant slip varies widely (Fig. 21A–C), sometimes merely having vestigial residues due to exposure of the sherds' surfaces to weathering. Some surfaces are eroded to the point where temper becomes visible; temper can include quite large pieces (Fig. 21J–L). One red-slipped (2.5 YR 5/8) surface sherd (Fig. 21H) is a handle fragment of the "monkey," a water jug of the colonial era. Another piece exhibiting three finger-indented surfaces (Fig. 21I) is a coal-pot grate remnant. The three indentations penetrate the artifact between its top and bottom surfaces and they correspond to holes poked by fingers through the clay, when in its plastic state, to form the grate. When charcoal was ignited on the grate, these holes circulated air to the fire. According to Heath (1988:115, fig. 3–22), the clay grate, known as a "bar," is distinctive to Antiguan coal pots. Informants said that coal pots and ceramic containers produced at Sea View Farm were shipped regularly to Barbuda in the past, and many of the surface-collected Codrington Castle sherds are virtually indistinguishable from Sea View Farm sherds observed on Antigua by the author. There is no evidence that pottery ever was made on Barbuda, either in the historic past or in recent times.

Ceramics of Uncertain Origin.—Classification of 16 excavated and six surface-collected sherds is more nebulous. Certain attributes preclude the assignment of these sherds to imported ceramics and certain technological aspects preclude their assignment to Afro-Caribbean (West Indian-origin) ceramics. These 22 sherds, which are confirmed or inferred to be both wheel made and kiln fired, are segregated into three groups designated Category A, B, or C (Table 8) in this paper.

Category A consists of six unglazed sherds thoroughly fired in a kiln to a generally reddish color (uniform throughout the paste). They are presumed to be wheel made (there is no evidence of coiling); however, the paste is less fine grained than in the other wheel-made ceramics. In their overall appearance (Fig. 22A–D), these six sherds bear the closest resemblance to the thinner Afro-Caribbean sherds, but their manufacturing technology (being wheel made and kiln fired) does not equate with the coil-built, open hearth-fired African pottery-making tradition.

Eight sherds are segregated in Category B because they are glazed (Fig. 22E–H). Two have yellow (5 Y 7/8) glaze, including an incompletely fired rim with an interior glaze and parallel striations on its exterior. Three sherds are more reddish colored, one of which (FSN 236) has fine-grained reddish yellow (5 YR 6/8) paste and a glaze partly exfoliated (Fig. 22H). Its paste is identical to six unglazed sherds discussed in Category C. Three conjoining sherds have a strong brown (7.5 YR 5/6) interior glaze, fine-grained dark gray (2.5 Y 4/0) paste, and a reddish brown (5 YR 5/4) unglazed exterior. They are noteworthy because one sherd (Fig. 22F) occurred immediately atop (Stratum II) and two (Fig. 22G) were directly below the floor in level 4 of Stratum III (Fig. 12). This was the sole case of articulatable artifacts found above and beneath the floor. Category B sherds can be readily segregated from imported sherds, despite their same attributes of

←

gray stoneware with embossed lion-like emblem (T44), surface (FSN 366 and 367); K, green-glazed, cream-bodied refined earthenware (T33), level 2 (FSN 94); L, untyped lead-glazed redware (probably French), atop floor (FSN 176); M, overglaze enamelled Chinese export porcelain (T26), atop floor (FSN 177).

Table 10.—*Manufacturing date ranges and median dates for excavated typed ceramics. Mean date: $51,025 \div 29 = 1759.48$ or 1759 (if type 65 is excluded, as South [1977:213] suggests, the mean date becomes 1772.05 or 1772, a difference of 13 years).*

Type number ^a	Range ^a	Median date ^a	Count	Product
65	1640–1800	1720	7	12,040
39	1660–1800	1730	1	1730
26	1660–1800	1730	1	1730
56	1670–1795	1733	3	5199
54	1690–1775	1733	1	1733
49	1700–1800	1750	4	7000
40	1720–1805	1763	1	1763
33	1759–1775	1767	1	1767
22	1762–1820	1791	3	5373
20	1780–1830	1805	2	3610
19	1780–1830	1805	4	7220
2	1820–1900	1860	1	1860
Totals			29	51,025

^a After South (1977:table 31).

being wheel made, kiln fired, and glazed, because they differ so much in appearance (Fig. 19, 22). In general, Category B sherds appear to be utilitarian. Although Category B sherds appear less refined than imported ceramics, the possibility that some Category B sherds are of European manufacture cannot be ruled out because their production locales are uncertain.

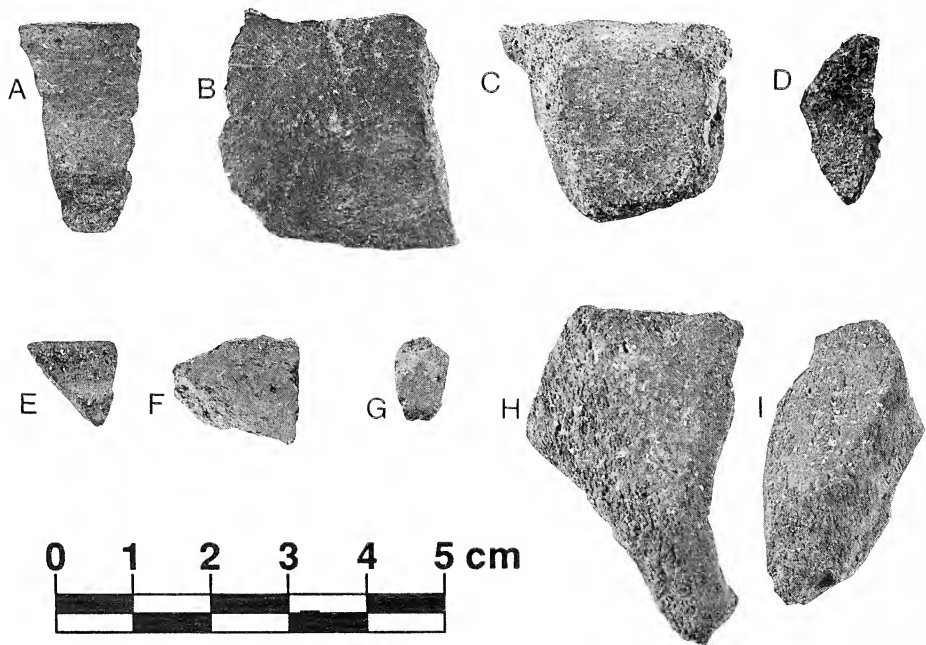


Fig. 20.—Excavated Afro-Caribbean sherds from Codrington Castle. A, rim (FSN 180), atop floor; B, body (FSN 179), atop floor; C, body (FSN 43a), level 1; D, body (FSN 182), atop floor; E, rim (FSN 43c), level 1; F, body (FSN 43e) with burnishing, level 1; G, body (FSN 43b) with vestigial slip, level 1; H, body (FSN 121), level 3; I, body (FSN 100), level 2. H and I conjoin.

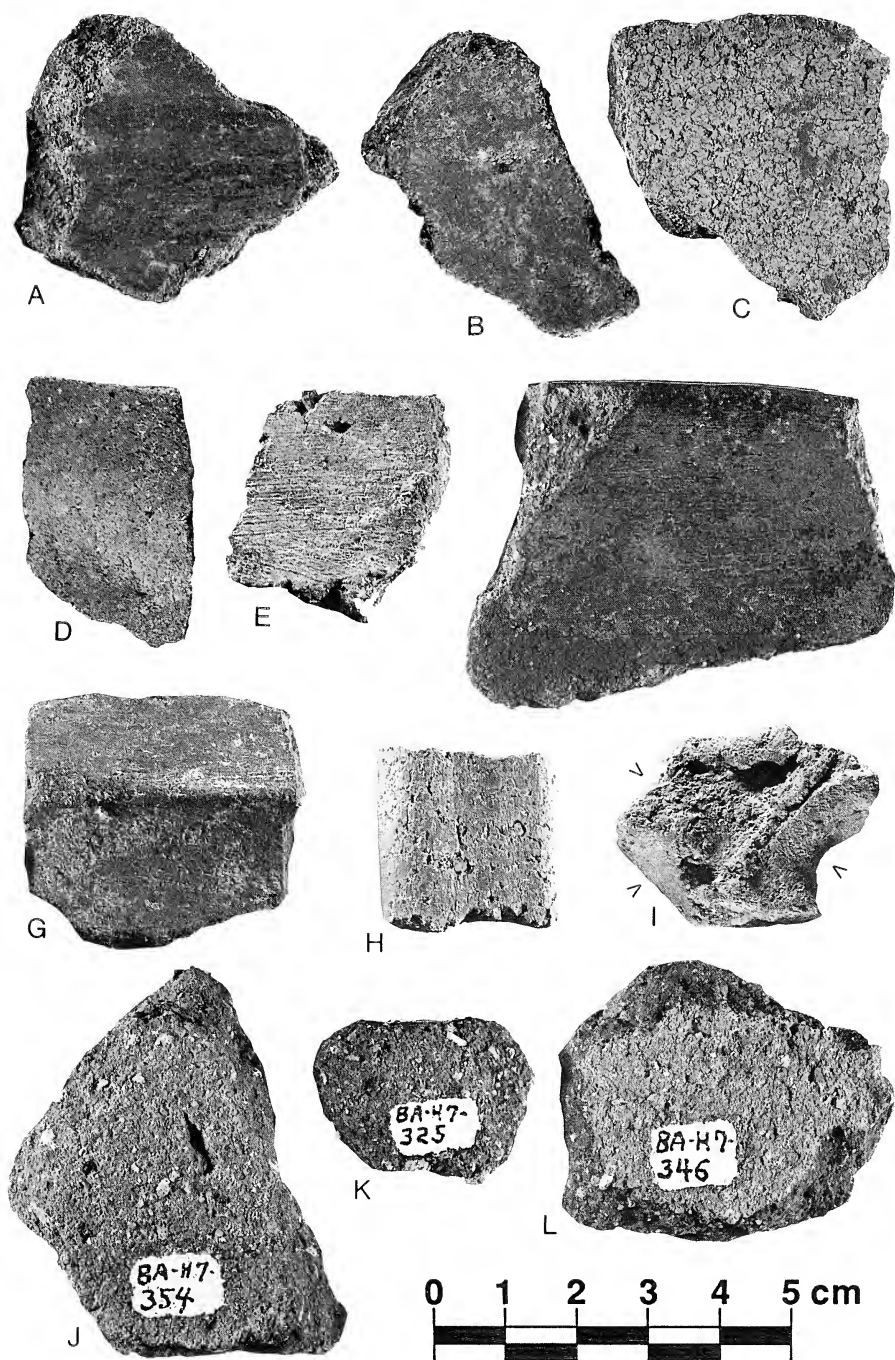


Fig. 21.—Surface Afro-Caribbean sherds from Codrington Castle. A–C, body sherds (FSN 347, 336, 340) showing varying retention of red slip, from fully preserved to partially eroded to patchy remnants; D, unslipped body (FSN 359); E, body with a cream-colored precipitate (FSN 331); F, G, rims with reddish brown slips (FSN 357 and 345); H, “monkey jar” handle fragment (FSN 328); I, three finger-indented (indicated by arrows) surfaces of a coal-pot grill (“bar”) fragment (FSN 343); J–L, exfoliated surfaces of body sherds with visible temper (FSN 354, 325, 346). A–C, F, I, and J–L are Sea View Farm pottery made on Antigua.

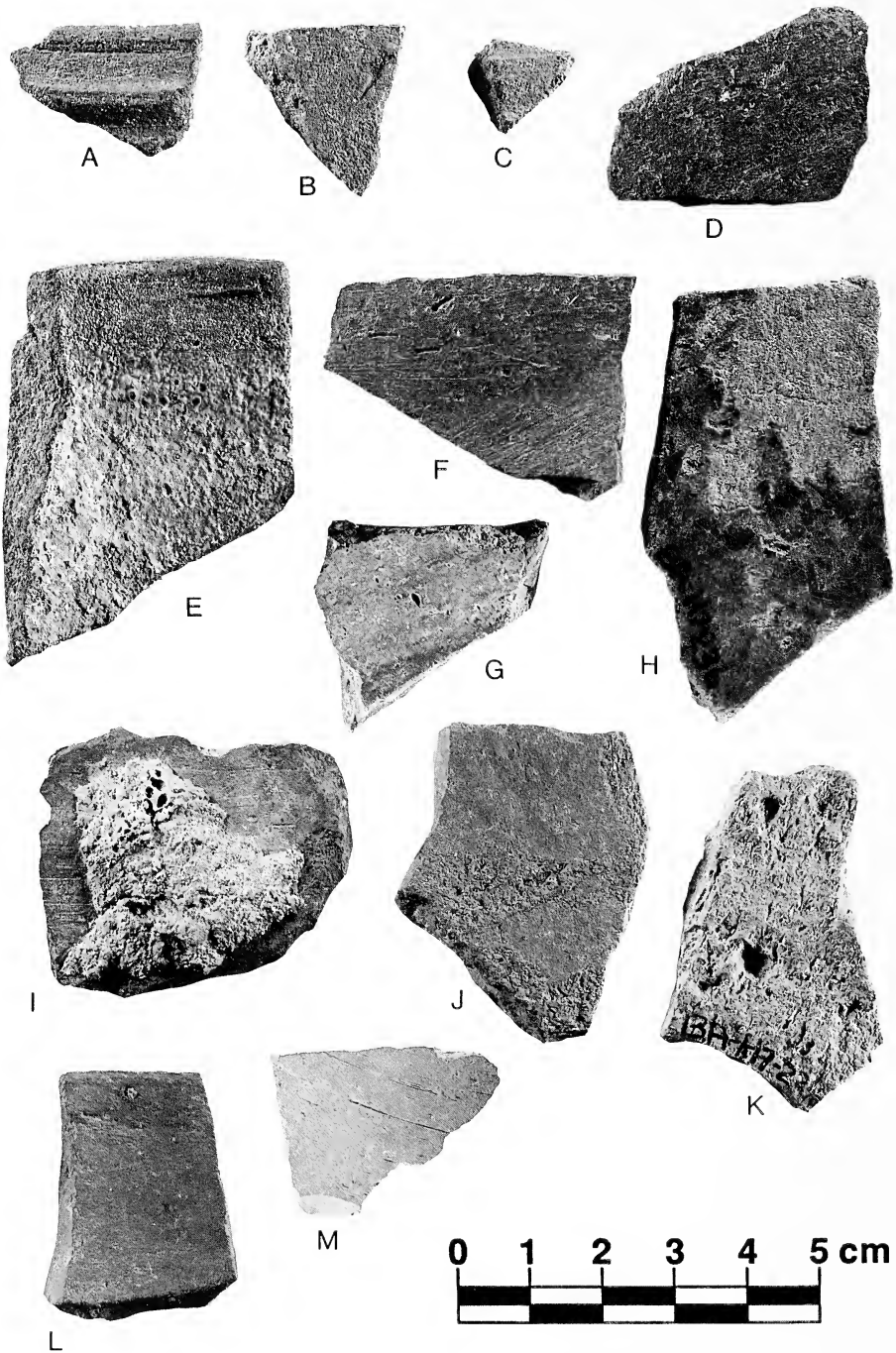


Fig. 22.—Ceramics of uncertain origin. Category A sherds: A, rim (FSN 101a), level 2; B, body (FSN 224b), level 4; C, body (FSN 43d), level 1; D, body (FSN 101a), level 2. Category B sherds: E, yellow-glazed rim (FSN 234), level 4; F, G, two conjoining body sherds (FSN 181 and 235) with unglazed exteriors and glazed interiors, found atop floor and in level 4; H, partly exfoliated glazed body (FSN 236), level 4. Category C sherds: I, body sherd with adhering pink

Category C includes two conjoining excavated (Table 8) and six surface-collected (Table 1) sherds. All are unglazed. They display dark gray (10 YR 4/1) exteriors with red (10 R 5/8) splotches and cores with bands of light brownish gray (2.5 Y 6/2) and light red (7.5 R 6/6); their interior surfaces are eroded completely to the core (Fig. 22K). The six surface sherds are alike in having very fine-grained reddish yellow (5 YR 6/8) to yellowish red (5 YR 5/6) pastes (Fig. 22I, J, L, M). Sherds so colored (they appear "orange") are derived both from containers and tiles, and they commonly occur in West Indian historic sites. Two sherds (Fig. 22M) have slips (not glazes) ranging from very pale brown (10 YR 7/4) to reddish yellow (7.5 YR 6/6). Adhering to another sherd (Fig. 22I), including one of its broken edges, are pink clumps identical in color (5 YR 7/3) to the previously discussed plaster, indicating this piece likely was used for chinking.

Afro-Caribbean and Categories A, B, and C Ceramics

The Ceramic Artifacts section purposefully contrasted the traditions represented respectively by wheel-made, kiln-fired, glazed imported ceramics and coiled, open hearth-fired, unglazed Afro-Caribbean pottery; it also intentionally placed Category A, B, and C sherds in an intermediate position that does not conform precisely to either tradition. This strategy was adopted because it facilitates discussion of the syncretism of these traditions, the ethnicity of the potters, and the probable places of pottery manufacture.

Within the British West Indies, Barbados provides the best documented case of potters of African heritage using European derived wheel and kiln pottery manufacturing technology. Handler (1963*a*, 1963*b*; Handler and Lange, 1978:139–144) argues that the wheel and kiln technology initially was introduced to Barbados by European indentured servants; later, enslaved Africans working on the sugar estates learned the wheel and kiln technology. Most of the ceramics produced were for plantation use (e.g., sugar pots) and domestic purposes. Thus, the European technology has been used by African potters and their descendants on Barbados up to the present day (Handler, 1963*b*). Also of interest is that most Barbados potters have been men. The recent pottery of Antigua and Nevis and its historical antecedents stand in sharp contrast to the findings on Barbados. Antiguan and Nevisian pottery has been manufactured exclusively in the hand-built and open-fired African tradition, and it is women who are the potters on these islands (Handler, 1964; Heath, 1988; Olwig, 1990). As defined by Petersen and Watters (1988), the term Afro-Caribbean pertains to the Antigua and Nevis ceramics because they are derived from the African pottery-making tradition, but Afro-Caribbean does not apply to wheel-made Barbados ceramics derived from the European tradition, even though the potters of Barbados were of African heritage.

The proximity of Antigua to Barbuda and the historical ties of the Codrington family to both islands logically would account for the presence of coiled, open-fired, unglazed Afro-Caribbean sherds found at Codrington Castle. Nevertheless, the possibility that some are Nevisian ceramics cannot be ruled out. The thicker post-emancipation Sea View Farm pottery on the site's surface as well as inform-

←

plaster (FSN 365), surface; J, body (FSN 361), surface; K, body with eroded interior (FSN 224a), level 4; L, rim (FSN 364), surface; M, slipped body sherd (FSN 362), surface.

ants' statements about the continued importation of Antigua ceramics during the recent past indicate the persistence of this Antigua connection.

However, the Codrington link between Antigua and Barbuda does not account for the presence of the categories A–C wheel-made, kiln-fired sherds at Codrington Castle, since the European pottery-making tradition was not practiced, or at least has not yet been documented, on Antigua during the historic period. One possible source for at least some of these ceramics of uncertain origin might be Barbados, and again there may be a connection to the Codringtons. Handler (1963a:135–138) documents the existence of a “pot works” at Consett Estate, the estate to which Christopher Codrington (III) retired from Antigua and where he died in 1710. Importation of wheel-made pottery from Barbados for use at the Codrington estates on Antigua is plausible, as is its subsequent shipment to Barbuda. Loftfield's (1994:6) small-scale testing of the Codrington Pottery Manufactory at Consett estate indicates the potential of a systematic study of these ceramics. Consett estate's pottery is highlighted because of its ownership by the Codringtons, but ceramics were being produced at other centers on Barbados as well (Handler and Lange, 1978:table 13; Loftfield, 1991).

Antigua is a second possible source for wheel-made pottery found on Barbuda. Desmond Nicholson (personal communication, 1994) informed the author that there was an area in Antigua, not far from the Codrington estate at Betty's Hope, known historically and to the present as “pots work” (in the Antiguan dialect; rather than “pot works”). Nicholson suspects this location was a center for ceramic production prior to emancipation. Whether the pottery produced here was wheel made or hand built is unknown. If the Codringtons owned this pottery, it is plausible to suggest they may have introduced the wheel-made pottery technology to Antigua from their Barbados estate. This line of reasoning is admittedly tenuous, but the existence of this site is worth mentioning because it has not been reported previously. Field research at the “pots work” site to investigate these issues unfortunately will be made more difficult by its inundation in the 1970s by a reservoir.

Finally, ceramics were produced in other British West Indies islands, such as St. Lucia and Jamaica (see Heath, 1988:124–132), in Danish (Gartley, 1979), French (England, 1992), Dutch (Heath, 1988), and Spanish (Joseph and Bryne, 1992; Crane, 1993; Rivera Calderon and Solis, 1993) islands, and various countries in Europe for export to their colonies in the Caribbean. While the manufacturing centers for categories A–C sherds found at Codrington Castle cannot be established with any degree of certainty at this time, the range of issues involved in such determinations and the suggested alternative hypotheses, which all too often in the past have been neglected or ignored, merit further investigation and deliberation.

Faunal Remains

Vertebrate and invertebrate faunal remains from BA-H7 are summarized but not tabulated because a comprehensive treatment, which combines faunal data from excavations at Codrington Castle and Highland House (BA-H1), will be published separately. The Codrington Castle vertebrate fauna, studied by Elizabeth J. Reitz, primarily includes domesticated animals such as pig (*Sus scrofa*), cow (*Bos taurus*), goat (*Capra hircus*), sheep (*Ovis aries*), and chicken (*Gallus gallus*) as well as a small number of nondomesticated bird, reptile, and fish remains. The

bivalve and gastropod faunas studied by Edward J. Petuch included some specimens indicating live capture and others gathered post-mortem. White mortar adhering to many dead specimens indicates they were components of the Stratum II floor, and not deposits of food remains. One branching coral fragment and three crab remains were recovered in test pit 1.

Analysis of Stratigraphy and Chronology

Of the 1107 excavated artifacts, three were pieces of the Stratum II floor and 1104 artifacts came from the unconsolidated sediments in strata I and III (Fig. 12).

Table 11 tabulates the 1107 artifacts by stratum and level. Structural artifacts ($n = 557$; 50.3%) are most abundant followed by glass ($n = 273$; 24.7%), metal ($n = 182$; 16.4%), ceramic ($n = 71$; 6.4%), kaolin pipes ($n = 14$; 1.3%), and flint/chert ($n = 10$; 0.9%). Each artifact category is represented in every level of test pit 1 with two exceptions, flint/chert in level 1 and kaolin pipes in level 3; likewise, the consolidated matrix floor samples are present only in Stratum II.

Table 11 also tabulates artifacts by their position above the floor, combining Stratum I (levels 1–3) and Stratum II (atop floor), and below (Stratum III, levels 4–5). The combined total above-floor artifacts ($n = 947$; 85.5%) greatly exceeds the below-floor total ($n = 157$; 14.2%); floor matrix samples are ignored. However, the inclusion of structural artifacts heavily skews the above-floor percentage. Even when all structural components ($n = 557$) are eliminated, leaving 550 non-structural artifacts, a sizable disparity persists between above-floor ($n = 421$; 76.5%) and below-floor ($n = 129$; 23.5%) artifacts.

Test pit 1 has been minimally disturbed by recent intrusion. Modern artifacts, such as the colored bottle glass (Table 3) and certain metal items (Table 6), are restricted to the upper 10 cm of the test pit. Level 1 also contained the youngest datable imported sherd, the Type 2 whiteware sherd with a median date of 1860 (Table 10). Below level 1, all artifacts are historic-era materials.

Stratum II is a distinctive feature of one construction episode at the Castle. This floor, an impenetrable consolidated matrix 5–8 cm thick, seals the deposits below. Stratigraphically it provides a chronological marker by separating the two artifact-bearing strata (Fig. 12). The distribution of datable artifacts above and below Stratum II provides a means for extrapolating the time period when the floor was constructed.

The three datable bottle glass fragments are in proper stratigraphic and chronological order. FSN 216 (dated to the mid-18th century) and 217 (ca. 1730–1785) occur below the floor in level 4; FSN 157 (ca. 1790–1820) was situated immediately atop Stratum II (Table 3, 4). The intact kaolin pipe bowl (ca. 1645–1665) comes from level 5, the deepest part of test pit 1; older pipe stems with larger-bore diameters (ca. 1680s–1750s) exist under and above the floor, but the smallest diameter (4/64 in) stem, prevalent after ca. 1750, appears only above (Table 5).

The 29 typed imported ceramics and their manufacturing spans and median dates also bear on chronology. Of three (T65, T49, T54) below floor-typed ceramics, two (T65 and T49) also occur above, in Stratum II immediately atop the floor (Table 9). All three types have median dates of 1750 or before and very lengthy manufacturing ranges (Table 10). Two types (T26 and T56) located immediately atop the floor likewise have long manufacturing spans with median

Table 11.—Summary table of excavated artifacts at Codrington Castle, Barbuda.

Stratum/level	Structural	Glass	Kaolin	Metal	Flint/chert	Ceramic	Total per level		Total above/below	
							Count	%	Count	%
Above floor										
I/1	34	138	1	85	0	18	276	24.9		
I/2	65	14	2	32	4	14	131	11.8		
I/3	383	5	0	18	1	4	411	37.1		
II/atop	44	31	5	31	1	17	129	11.7		
Total above floor	526	188	8	166	6	53	3	0.3	947	85.5
Below floor									3	0.3
III/4	21	52	4	11	3	14	105	9.5		
III/5	7	33	2	5	1	4	52	4.7		
Total below floor	28	85	6	16	4	18			157	14.2
Grand total										
Count	557	273	14	182	10	71	1107			
%	50.3	24.7	1.3	16.4	0.9	6.4		100.0		

dates respectively of 1730 and 1733. These five types have manufacturing ranges starting between 1640 and 1700. Beginning with level 2 (10–20 cm) in Stratum I, a definite shift is evident to typed ceramics having younger median dates and with manufacturing ranges that start no earlier than ca. 1720 (with one exception, T39). Level 2 is marked by one type (T33) having a narrow (1759–1775) manufacturing span, by the first appearance of creamwares (T22) and pearlwares (T19 and T20), and the absence of older slipware and delftware (T56, T49, T65) ceramics (Table 9).

Manufacturing spans for artifacts beneath the floor begin as early as the 1640s (pipe bowl and T65) and continue as recently as about 1800 (T65, T49). However, the glass and pipe artifacts in particular imply a more restricted span, from the mid-17th to mid-18th centuries (ca. 1650s–1750s). Manufacturing spans for above-floor artifacts are predominantly from the middle and late decades of the 18th century (ca. 1730s–1800). The time span of level 2 clearly is latter 18th to early 19th century. Artifacts from the basal level of Stratum I, immediately atop the floor, include glass, kaolin pipes, and older ceramics types which were still being manufactured in the first half of the 18th century; but artifacts atop the floor do not include any of the younger ceramic types (i.e., manufacturing ranges beginning in the 1750s) found in the levels above. These data indicate that Stratum II, the floor matrix, was constructed during the first half of the 18th century (1700–1750). A narrower time span of construction is more problematical, but the data suggest the floor probably was built between 1720 and 1750.

In summary, stratigraphic and chronological data in test pit 1 indicate that Stratum III represents a latter 17th- to early 18th-century deposition, followed by construction of the Stratum II floor in the first half of the 18th century, after which Stratum I was deposited in the latter half of the 18th and early 19th centuries. The implications of the test pit 1 data for the functions, construction, renovation, and destruction of the Castle are explored in the following discussion sections.

DISCUSSION AND INTERPRETATION

Functions of the Castle

Codrington Castle was a multipurpose facility throughout its existence. Tweedy's (1981:169) contention that the Castle was used principally for storage and as a residence, although it was originally intended primarily as a fortress, is a fitting characterization of its major functions.

Storage.—Codrington Castle served as a facility for the storage and transshipment of supplies and goods being imported and exported from Barbuda. Liggins (1837) alludes to the kinds of products stored in the Castle when he said it was no longer fit to receive and store a crop. Other stores included products from the industrial facilities (e.g. the tannery and rope house) in Codrington village and such commodities as wood and charcoal obtained elsewhere on the island. Materials imported from the Codrington estates on Antigua for distribution to the village's inhabitants would have been stored at the Castle as well.

In addition to routine commodities and supplies, the Castle stored goods salvaged from ships wrecked on Barbuda's dangerous reefs until those items could be shipped to Antigua for sale. Depending on the location of the wreck site, salvaged goods could be shipped from the wharf in the lagoon adjacent to the Castle, the landing at River (Fig. 2:BA-H2) on the southwest coast, which was



Fig. 23.—River Fort (BA-H2), consisting of a martello tower and attached gun platform, defended the major anchorage on the southwest coast of Barbuda. The white painted section facing seaward serves as a navigation aid.

defended by a martello tower and gun platform (Fig. 23), or Gravenor Bay on the southeast coast guarded by the Spanish Point structure (Fig. 2:BA-H3). These areas were linked by Barbuda's road system (Admiralty Hydrographic Office, 1814, 1850) and, according to James Goodlet (cited in Norie, 1836:[I]34), master of the *Jean Stewart*, a vessel wrecked on Barbuda in 1834, the road between Codrington village and River landing was a very good one.

Glazed and unglazed ceramic containers from test pit 1 can be interpreted as evidence of the Castle's function of storing commodities, although they could have served other purposes as well.

Administration and Habitation.—The Castle also served, especially in the early years, as the administrative center for the island and as a residence for managers. Codrington Castle provided lodging for visitors to Barbuda including de Ponthieu in 1780 and the Coleridge party in 1825. Coleridge (1832:263) noted that Mr. James, the Codrington attorney, and his family stayed at the Castle while visiting from Antigua. The Castle accommodated white overseers as late as 1840 according to the two magistrates visiting from Antigua.

A separate residence had been built by one manager, Samuel Redhead, by the 1770s (Tweedy, 1981:42); he probably was not the first manager to do so. This residence would be the structure termed the "mansion" that serves as the focal point in the 1818 painting (Fig. 8). In 1813, after H. M. S. *Woolwich* ran onto a reef during a hurricane, its crew was housed at the Castle while the officers lodged with the resident manager (Tweedy, 1981:167, fn. 64), an arrangement that un-

doubtedly was agreeable with the officers in view of Captain Greville's comment about the Castle being dilapidated.

The Castle's residential function as a place of lodging is confirmed by test pit 1 artifacts. These include glass bottles containing beverages, kaolin pipes for smoking, and the imported European and Chinese ceramics and domestic Afro-Caribbean sherds for serving and preparing food. The small gunflint suitable for a fowler or rifle (but not a musket) arguably reflects a related recreational function, for which historical documents attest to fowling by the Coleridge party and deer-hunting by officers of H. M. S. *Woolwich*, among others.

Defense.—The Castle served as the principal venue for defense and refuge during times of trouble, which were virtually uninterrupted by peace in the earlier years of the Codrington lease. The change in enemies, tactics, and weapons in a single century, between the 1680s when the Castle was first built and the 1780s when Henri de Ponthieu visited Barbuda, is mirrored in the amateur botanist's comment that the Castle may have served its purpose in the past, defending against Indians, but would no longer stand up against Europeans and their weapons (Tweedy, 1981:235). Carib Indian raids, prevalent in the middle decades of the 17th century, continued at least until 1681 (Burns, 1965:345; Watters, 1980a: 88). A fleet of buccaneers reportedly landed on Barbuda in 1687 while John Codrington was living there (Harlow, 1990:190, fn. 2). In 1689, a rebellion by Irishmen (presumably indentured servants) on Barbuda was suppressed; that same year, a force of invading Frenchmen and escaped Irish indentured servants was put to flight (Harlow, 1990:17).

France and England were almost constantly at war from 1689 until 1713, and their Caribbean colonists became embroiled in the hostilities by launching attacks against each other's islands. During this strife-torn period, two Christopher Codringtons (II and III), both being lessees of Barbuda, served successively as the military Captain-General and administrative Governor-in-Chief of the Leeward Caribbean Islands (Oliver, 1899:[III]318). Each resided at Betty's Hope on Antigua, the island from which they led assaults, respectively in 1691 and 1703, against Guadeloupe, Antigua's neighboring French island. In February 1705, Père Jean Baptiste Labat witnessed a French raid on Barbuda, the object of which was capturing Christopher Codrington (III), in reprisal for his 1703 invasion of Guadeloupe. Although the French force was unable to apprehend Codrington since he had already departed for Antigua, it was able to inflict considerable damage by pillaging Codrington's house, seizing his belongings, and capturing 15 slaves (Eaden, 1931:250–251). Barbuda also was drawn into conflicts between countrymen. There is one record (Dunn, 1972:145) of a raid by privateering henchmen operating under the auspices of Daniel Parke, the new Governor-General of the Leeward Islands Colony, who in 1707 tried to dispossess Christopher Codrington (III) of Barbuda (Harlow, 1990:190).

As the principal place of defense on Barbuda, the Castle would have been the scene of skirmishing and perhaps full-scale assaults during some of these hostilities. It assuredly was the target of a major French attack in March 1710. During a surprise attack, the French forces blew up the Castle and carried off the island's inhabitants (Oliver, 1894:[I]169; Tweedy, 1981:14, 35). Barbuda was briefly occupied by two privateers in November 1710 and Spanish privateers captured ships near the island in 1743 and 1779 (Oliver, 1894:[I]xxxix; Tweedy, 1981:35–36).

The Castle figured prominently in another violent incident in Barbuda's history, although this event was an internal one. On December 22, 1745, the slaves on

Barbuda rebelled and killed the manager, a man named McNish (Tweedy, 1981: 37–38, 190–191). Although the immediate impetus for the revolt seems to have been McNish's order to mutilate two slaves for stealing sheep and cattle, it is likely that the barbaric treatment of some slaves by another manager, Thomas Beech, during preceding years (based on depositions made in 1741) was a contributing factor (Tweedy, 1981:190). The slaves successfully occupied the Castle and took possession of its arms and ammunition. To put down the rebellion required troops from Antigua, which had experienced its own well-organized but unsuccessfully executed revolt led by Court (alias Tackey) only nine years earlier (Gaspar, 1985). The leaders of the Barbuda slave revolt were burned alive in front of the gate of the Castle. The inaccessible Codrington Papers most likely record the identities of these courageous leaders although their names currently are unknown. This event surely was an influence on the Codrington family's decision in 1746, the year following the rebellion, to sublet Barbuda to Martin and Byam for 15 years.

The only test pit 1 artifacts potentially related to the defense function are two lead lumps (for making bullets) and the gunflint.

Construction and Renovation

Codrington Castle functioned as it was intended for more than two centuries, from its initial construction in the 1680s until it was demolished near the start of the 20th century. John Codrington's decision to build the Castle reflects the troubled times of the late 17th century, and his conviction was certainly justified in view of raids made on Barbuda by Caribs, buccaneers, and French and Irish forces during the decade of the 1680s alone. This first Castle, completed by about 1688, the year John died on Barbuda (Harlow, 1990:15, 190), was the building destroyed in the French attack of 1710. The first Castle also was referred to in a new lease authorized by Queen Anne for Christopher Codrington (III) in 1705 "in consideration of [his] service. . . and of his having built a castle on the said Island which was defended at his own cost and expense" (Hall, 1971:59).

John's son, William, who inherited Barbuda from his cousin Christopher Codrington (III), was responsible for completing the second Castle "at very great expense" (Tweedy, 1981:35). Exactly when the second Castle was finished is uncertain; it probably was rebuilt by 1720, although Nicholson (1979:55) suggests a slightly later date of 1728. William had lived in the West Indies during his youth, perhaps even on Barbuda with his father, but by 1717 he was residing in England (Tweedy, 1981:14–16). William, being the last Codrington to spend an appreciable part of his life in the West Indies, represents the beginning of the transition to absentee ownership. His desire to return to the West Indies, as he revealed in his letters (cf. Oliver, 1894:[I]170), was the stimulus for starting construction at Highland House, an 18th-century retreat (Watters and Nicholson, 1982:233), but William nonetheless died in England in 1738 (Oliver, 1894:[I]150–151).

William wanted to further fortify Barbuda, but the project was completed mainly after his death. Two individuals, Benjamin King, the Codrington attorney on Antigua, and Simon Punter, the new manager, were the persons responsible for the fortification project, which was planned by and carried out under the auspices of Admiral Knowles, commander of the naval facility at English Harbour on Antigua (Nicholson, personal communication, 1994). Punter noted that Barbuda

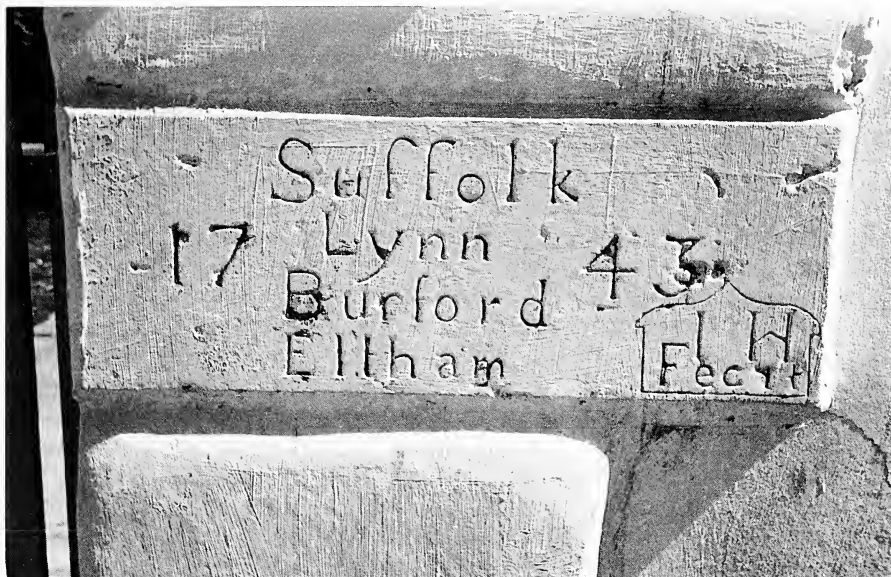


Fig. 24.—Commemorative stone tablet of four naval vessels involved in the 1743 fortification project on Barbuda.

had no means of protection except the Castle; upon his assumption of duty, Punter did what he could to strengthen the building (Tweedy, 1981:35). In 1743, King ordered three 12-pounder guns for a fortification he proposed to build, “. . . a tower like those on the coast of Spain. . .” (Tweedy, 1981:36), which undoubtedly refers to the martello tower located at River landing (Fig. 23). Coastal batteries were constructed as well. Maps in the Devonian Foundation folio (1988) show this system of fortifications. A carved stone tablet dated 1743 commemorates four of Admiral Knowles’ naval vessels—*Suffolk*, *Lynn*, *Burford*, and *Eltham*—stationed at Barbuda during the project. The stone, presently embedded in a wall at the Warden’s House (Fig. 24), originally was situated in the Castle according to Barbudans.

During the remainder of the 18th and early 19th centuries, the attention given to the Castle’s state of repair reflects the capabilities of various managers. Managers administered the day-to-day operation of the island largely on their own, apart from infrequent trips made by Codrington attorneys from Antigua and even rarer visits by family members from England. By then the Codringtons were fully absentee leaseholders. Correspondence from this period, used by Tweedy (1981) for her thesis, documents highly variable administrative abilities on the part of managers and attorneys. The Castle’s existence is confirmed by specific references to it in a set of legal indentures dating from 1763, 1764, and 1776 (Oliver, 1894: [I]153–154). There is no evidence the Castle was destroyed during the late 18th and early 19th centuries; instead, it was subject to periods of neglect by indifferent managers interposed with periods of maintenance and renovation by competent and conscientious ones. In 1829, the Codrington family attorney on Antigua, Robert Jarritt, described Barbuda as being neglected, with dilapidated fences, gates, and buildings (Tweedy, 1981:111). Greville’s 1813 observation (in Southey, 1968) of an old dilapidated castle suggests the structure had been neglected, as

does Liggins' comment in 1837 about it being in ruins. Yet, Codrington Castle was in a good enough state of repair to have lodged de Ponthieu in 1783 and Coleridge in 1825.

The Castle was severely damaged if not completely destroyed on February 8, 1843, when a very strong earthquake, centered in the Leeward Islands, extensively damaged masonry buildings on Antigua, Montserrat, St. Kitts, and other nearby islands (Robson, 1964:798–800). Christopher William Codrington contended that the earthquake had razed Codrington Castle to the ground and that he had ordered the building repaired, but since he made that claim in 1854, while applying to the Crown for renewal of his lease, the degree of damage (and extent of repair) may be embellished somewhat. Natural disasters probably damaged the Castle at other times, particularly in view of the prevalence of hurricanes and earthquakes in the region, but the damage in 1843 is the only episode so far documented. A May 20, 1895, earthquake cracked walls in the church and lessee's house in Codrington village but there is no mention of damage to the Castle (Robson, 1964:808).

It is for the Castle's construction and renovation phases that artifacts from test pit 1, along with their stratigraphic positions and chronology, provide the most detailed findings to augment the architectural information from historical records. Stratum II represents an early to mid-18th century renovation in which the dense matrix was laid down to create a new floor, at a time period that corresponds well with construction of the second Castle by William Codrington in the 1720s. Artifacts sealed in Stratum III beneath the floor logically would associate with the occupation of the first Castle, from ca. 1688–1710. Stratum I shows no evidence of any structural renovation; its homogeneous sediments represent a gradual accumulation of deposits throughout the later 18th and the 19th centuries. Structural artifacts from test pit 1 provide data about the Castle's architectural features which are omitted in historic documents. Archaeological research alone confirms the surface coating of the limestone walls with a pink plaster applied atop a base of white mortar, the presence of glazed windows (the flat-glass category) and slate roofs, the use of bricks or clay tiles as indicated by the fired clay lumps, and the reuse of broken utilitarian pottery as chinking.

Destruction

A third Castle had been constructed following the 1843 earthquake according to Christopher William Codrington's lease renewal application of 1854. The true extent of this rebuilding effort is suspect because the sugar industry, the foundation of the Codrington family's involvement in the West Indies, was by then in decline. By 1843 the inhabitants of Barbuda and Antigua, already having been emancipated, were no longer the property of the Codringtons. In 1870, only 16 years after the lease was renewed, the Codrington family surrendered its final leasehold to Barbuda. At this same time references to the Castle disappear from visitors' accounts. The third Castle probably was a smaller and much less impressive structure.

This third Castle gradually deteriorated in the last half of the 19th century. The structure was extant in some form in 1870 when the Crown, in authorizing the new lease for Hopkins and Cowley, reserved parts of the Castle for its own use. Walbrook's childhood memory of the Castle confirms its existence until the late 1890s or early 1900s. The lack of reference to the Castle by visitors after about

1870 probably reflects the building's state of disrepair, in the sense that it no longer warranted comment. Barbudan informants say the ginnery was constructed with stones taken from the Castle; it is likely that stones were being removed even earlier to build houses in the village.

Walbrook's interview also provides a lead about the razing of the Castle, when he identifies a Mr. Dougal as the person in charge of Barbuda when the Castle was destroyed, which resulted in Dougal being sent away (*The Barbuda Voice*, 1971:2). Barbuda was leased from 1884 to 1891 by a William Dougall and then by his brother Robert from 1892 to 1898 (Hall, 1971:90–91; Berleant-Schiller, 1978:29–30). Hill (1898:322) mentions a Donald Dougald on Barbuda during his visit. Dougal, Dougall, and Dougald would seem to be simply spelling variations of the same surname.

Robert Dougall's leasehold coincides with Walbrook's early childhood and the 1895 earthquake on Barbuda. If Robert Dougall started to dismantle an earthquake-damaged, structurally unsound Castle in the final years of the decade of the 1890s, just prior to losing his lease, then Walbrook's remark about a Mr. Dougal being sent away because he destroyed the Castle is reasonable and logical.

The stratigraphic distribution of two kinds of structural artifacts, plaster and slate, confirm the deteriorating condition of the Castle. Table 2 shows the counts and percentages of plaster fragments in the two upper levels (9 and 45 pieces; 1.9% and 9.3% respectively) decrease dramatically from those in level 3 ($n = 370$; 76.4%). When plaster fragments from atop the Stratum II floor are added to level 3, their combined quantity ($n = 407$) and combined percentage (83.6%) are even more striking. As the plaster began to separate from the walls, it fell atop and built up from the floor; the stratigraphic distribution could indicate either a gradual accumulation as the building deteriorated or an episode of rapid collapse. Regardless, the few fragments in the upper portion of Stratum I suggest most of the plaster already had pulled away from the walls before deposition of levels 1 and 2. The presence of 25 pieces of pink plaster in Stratum III, in the sealed deposit beneath the floor (Table 2), indicates this material had been used as a wall coating from the earliest times. Slate distribution is different. It exists only in upper levels of Stratum I, with most pieces (95%) occurring in the uppermost level (Table 2). This distribution indicates the roof gave way later, relative to the separation of the wall plaster. Razing of the building was the roof's final downfall. The presence of late 19th-century and modern artifacts, in the uppermost level of test pit 1 and on the ground surface of the sector formerly occupied by the Castle, indicates continued use of this area by Barbudans, especially their reliance on Castle Well as a water source until the installation of the piped water system in the 1980s.

The Castle, Codrington Village, and Other Historic Sites

The Castle was the dominant structure in Codrington. Yet, it was only one of numerous buildings in the village including the slaves' dwellings, manager's residence, and industrial facilities. The untitled and undated village map in the Devonian Foundation folio (1988) shows some 20 buildings of various sizes dispersed in clusters around the Castle.

In 1780, de Ponthieu mentioned the rope house, latrine for white people, pigeon house, carpenter's shop, belfry, sick house, a place for building boats, various animal pens, and houses for the principal carpenter and huntsmen (Tweedy, 1981:

199, fn. 10). Greville (in Southey, 1968:[III]523–524) in 1813 pointed out the barn-like house of the manager, stables, artificers' shops, and the Negro huts. Coleridge (1832:257) noted the village's locked crabberies in which the land crabs he was served were fattened. Wentworth (1834:[II]242) said there were the "farm-house looking building" for the manager's residence, a hospital, stables, and artificers' stores. Liggins (1837) mentioned a turtle crawl, tan-house (tannery), coach house, stable, Negro Town dwellings, wells and pens, walls and gates, and a church. The Antigua magistrates in 1840 commented on the proximity of the stone farm buildings to the Castle, the laborers' houses, and a building that served as a chapel and school (Hall, 1971:70).

Walbrook's plan (Fig. 10) depicts a circular pigeon house, the location, size, and shape of which correspond to the cistern (Fig. 25A) now present behind the ginnery. Blocks of chunky limestone visible beneath the cistern's eroded facade (Fig. 25B) are typical building materials of the Codrington period. Also, de Ponthieu's comment about a "round tower fashion" pigeon house (Tweedy, 1981:199, fn. 10) provides corroboration for the extant cistern being the renovated pigeon house of Codrington Castle.

Other industrial enterprises are alluded to by the trades listed for skilled slaves, which include blacksmiths, tanners, carpenters, seine-knitters, shoemakers, col-larmakers, ropemakers, coopers, basketmakers, shipwrights, wheelwrights, and masons (Tweedy, 1981:184). These tasks were performed in the village, in some instances in separate buildings (e.g., the tannery) but others probably in the Castle itself. Potters are absent from the trades list.

The association between Codrington Castle and three other historic sites located elsewhere on Barbuda—Highland House (BA-H1), River Fort (BA-H2), and Spanish Point structure (BA-H3)—has been discussed. A fourth site, the Coco Airstrip structure (BA-H10) located in southeast Barbuda (Fig. 2), also relates to the Castle.

BA-H10, a lime kiln (Fig. 26), is the logical source for the material used to create the floor (Stratum II) and to produce the pink wall plaster observed in the test pit. Filling the kiln and removing the finished material were assigned tasks for the slaves (Tweedy, 1981:180). Lime was a significant export for Barbuda; 556 hogsheads were shipped in 1743 alone (Lowenthal and Clarke, 1977:513). There are two documented cases (in the 1830s and 1860s) when Barbudans lodged formal complaints alleging they had been deprived of the lime needed to build and repair their homes (Hall, 1971:86; Lowenthal and Clarke, 1977:516). Leases awarded after 1870, after the surrender of the Codrington lease, reserved specifically for Barbudans the right to collect coral for making lime (Hall, 1971:93, fn. 75). The possibility that nearby conch shell piles, created by Barbuda's prehistoric inhabitants, may have been another source of raw material for the kiln has been noted (Watters et al., 1992:44).

Lime production at the BA-H10 lime kiln exemplifies the role Barbuda played in the broader holdings of the Codrington family. Although this commodity was produced and used on Barbuda, it also was shipped to the Codrington sugar estates on Antigua and even marketed elsewhere in the West Indies (Tweedy, 1981:138–139).

CONCLUSIONS

Codrington Castle refers not to a singular structure but instead to a succession of buildings constructed and renovated during a span of some 220 years. The



Fig. 25.—The historic “round-fashion” pigeon house now serves as a cistern. A, the circular cistern is situated north of the ginnery (cf. Fig. 10, 11). B, chunky blocks of limestone visible beneath the cistern’s facade.



Fig. 26.—West face of the Coco Airstrip lime kiln (BA-H10) with its brick-lined arch for removal of the reduced lime.

persistent use of the term “Castle” is the enduring link between the structure built by John Codrington in the 1680s and the building ultimately razed at the turn of the 20th century. The Castle itself was entirely rebuilt twice. Historical documentation and archaeological research confirm that the Castle, in its three iterations, was situated in the same sector of Codrington village on the lagoon’s eastern shore.

Two different orientations revealed in various documents indicate the Castle’s configuration changed through time. The older records which concern the second Castle consistently depict a rectangular structure with its greatest length oriented east–west. Later documents, which postdate construction of the third Castle, record a rectangular building having a longer north–south axis. Although orientations differed, the main entryway into the Castle always was depicted in the south wall.

Regularly recurring architectural features, regardless of the particular iteration, include towers, a principal doorway, windows, and the crenel and merlon battlements, the latter being referred to as embrasures in the written accounts and appearing as crenelated patterns on drawings. Documented archaeologically are glazed windows, slate roofs, and the persistent application of pink plaster on the limestone walls.

Also confirmed by archaeological research is the rebuilding of the second Castle with the spreading of the dense matrix of Stratum II to create the floor. This architectural element is a stratigraphic feature, sealing the deposits related to the first Castle, and a chronological marker distinguishing those artifacts associated

with the first Castle from those of the second. The dense matrix of Stratum II is not restricted to test pit 1. In 1992, this same matrix was identified in bulldozer scrapings on the east and west sides of the ginnery building which was being repaired at that time (Fig. 4B background). The recurrence of this dense matrix in three widely separated sectors indicates that Stratum II very likely is preserved throughout the grounds of the Castle.

This expansive subsurface feature would serve to delineate the entire configuration of the second Castle as well as its internal arrangement of rooms and facilities. The conclusion is that Stratum II is the key structural element for determining the orientation and configuration of the second Castle. In addition, differential distributions of various artifacts across Stratum II would serve to distinguish activity areas within the confines of the Castle.

Test pit 1 verifies the Castle's diversity of artifacts and the minimal disturbance to its archaeological deposits. Many of the artifacts are routinely encountered in historic sites of the British colonial period in the West Indies and North America. Yet the Codrington Castle artifacts, and the ceramic and lithic samples in particular, offer new insights into theoretical and analytical issues at the regional level.

Regionally, there is proposed the distinction between Afro-Caribbean ceramics, representing the unglazed, hand-built, and open hearth-fired African tradition of pottery making, and the categories A, B, and C ceramics characterized by wheel-made glazed and unglazed pottery, at least some of which reflect a syncretism whereby persons of African heritage produced pottery using a technology derived from Europe. This distinction is most marked in the contrasting technologies still employed by Antiguan and Nevisian potters on the one hand and by Barbadian potters on the other; a gender-specific corollary of respectively female and male potters persists as well. Also important analytically is the proposed colonial exploitation of West Indian chert sources, particularly those of Antigua, and the recycling of prehistoric stone artifacts and actual mining of Amerindian sites by historic-era inhabitants.

The Castle exemplifies the history of Barbuda under the Codrington leasehold. Built in the 1680s by John Codrington, the first Castle was willed to his brother Christopher (III) and then to John's son William, the last of the Codringtons raised in the West Indies. William built the second Castle in the 1720s. It was successfully seized by rebelling Barbudan slaves in 1745 and was the scene of execution of the leaders of that revolt. There followed interspersed periods of neglect and care by various managers, until the 1843 earthquake destroyed the second Castle. The third Castle was then built but it gradually deteriorated in the late 19th century. Evidence of this deterioration and of the final razing of the Castle near the turn of the 20th century is provided by the structural artifact distributions analyzed from test pit 1. Today, although its surface location is marked only by Castle Well and the former pigeon house, Codrington Castle still exists archaeologically through its subsurface structural features and artifacts.

Barbuda has been seen as a remote island somewhat removed from the mainstream of West Indian plantation studies. However, Barbuda was not isolated during the historic era; instead, for more than two centuries it was an integral part of the extensive holdings of the Codrington family in the West Indies. A greater understanding of Codrington Castle's importance and relevance is attained by interpreting this structure, and Barbuda's historic sites generally, within this broader regional context.

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THE MIDDLE AMERICAN GENUS *ONYPTERYGIA* DEJEAN
(INSECTA: COLEOPTERA: CARABIDAE: PLATYNINI):
A TAXONOMIC REVISION OF THE SPECIES, WITH NOTES ABOUT
THEIR WAY OF LIFE AND GEOGRAPHICAL DISTRIBUTION

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ABSTRACT

Keys, descriptions, and illustrations distinguish the known species of the Middle American genus *Onypterygia* Dejean (type species *Onypterygia fulgens* Dejean), and each taxon is characterized in terms of structural features of adults, habitat, geographical distribution, and chorological affinities. For allopatric species that are markedly similar in structural features, a hypothesis of phylogenetic relationship is postulated. Fifteen new species are described.

The species of *Onypterygia* are arranged in seven groups, sequenced according to judgment about extent of departure from a generalized platynine body plan (type areas for new species in parentheses): *O. famini* group, including *O. famini* Solier and *O. cyanea* Chaudoir; *O. wappesi* group, including *O. wappesi*, n. sp. (Mexico, Guerrero, Sierra de Atoyac); *O. amecameca*, n. sp. (Mexico, state of México, Amecameca); *O. atoyac*, n. sp. (Mexico, Guerrero, Sierra de Atoyac); *O. shpeleyi*, n. sp. (Mexico, Guerrero, Sierra de Atoyac); and *O. pacifica*, n. sp. (Mexico, Oaxaca, Sierra de Miahuatlán); *O. aeneipennis* group, including *O. batesi*, n. sp. (Mexico, Tamaulipas, Sierra Madre Oriental [Sierra de Guatemala]), *O. aeneipennis* Chaudoir, *O. cupricauda* Casey, *O. stenapteryx*, n. sp. (Mexico, Michoacán, Sierra Transvolcanica West), *O. pallidipes* Chaudoir, and *O. rubida* Bates; the *O. perissostigma* group, including only *O. perissostigma*, n. sp. (Mexico, Oaxaca, Sierra de Juárez), the *O. pusilla* group, including *O. pusilla* Chaudoir and *O. rawlinsi*, n. sp. (Mexico, Nayarit, Sierra Transvolcanica West); the *O. angustata* group, including *O. longispinis* Bates, *O. angustata* Chevrolat, *O. pseudangustata*, n. sp. (Mexico, Puebla, Sierra Transvolcanica East), and *O. sriblingi*, n. sp. (Mexico, Oaxaca, Sierra de Juárez); and *O. fulgens* group, including *O. iris* Chaudoir, *O. championi* Bates, *O. donato* Ball and Shpeley, *O. chrysura* Bates, *O. kathleenae*, n. sp. (Mexico, Oaxaca, Sierra de Juárez), *O. exeuros*, n. sp. (Mexico, Oaxaca, Sierra de Juárez), *O. polytrete*, n. sp. (Panama, Chiriquí Province, Talamanca Cordillera, Cerro Pando), *O. crabilli*, n. sp. (Costa Rica, Puntarenas Province, Talamanca Cordillera, Monteverde), *O. quadrispinosa* Bates, *O. scintillans*, n. sp. (probably Costa Rica, Talamanca Cordillera), *O. fulgens* Dejean, *O. tricolor* Dejean, *O. hoefpneri* Dejean, and *O. sallei* Chaudoir. New synonymy is as follows: *O. cyanea* Chaudoir, 1878 = *O. valdestriata* Bates, 1884; *O. fulgens* Dejean, 1831 = *O. thoreyi* Mannerheim, 1844; *O. tricolor* Dejean, 1831 = *O. apicalis* Chaudoir, 1837 = *O. tricolor* var. *dimidiata* Chevrolat, 1837. Other synonyms are as published by previous authors.

Geographical distribution of *Onypterygia* is analyzed in terms of altitudinal range, and nine areas of precincton, each of which is highland isolated by surrounding lowlands. The areas are, from south to north: Talamanca Cordillera; Chiapan-Guatemalan Highlands; Sierra Madre de Oaxaca; Sierra de Miahuatlán; Sierra de Atoyac; Sierra Transvolcanica East and West; Sierra Madre Oriental and Occidental. Seven areas have representatives of four to six species groups, but the northwesternmost (Sierra Madre Occidental) and southernmost (Talamanca Cordillera) have only two groups. At the species level, the northern centers (Sierra Madre Oriental and Occidental) lack precinctive species, but the southern Talamanca Cordillera has nine such species. Speciation, then, has been most frequent in the more southerly centers. Probably the northern centers have been invaded relatively recently, or evidence of older invasions has been lost because of extinctions.

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Speciation is postulated to have involved, during late Tertiary–Quaternary time, alternating sequences of geographical isolation (with consequent differentiation of the isolates) in the montane forested areas of precinction, followed by dispersals of previously isolated stocks. This explains both the extensive sympatry of the species groups (because of dispersal), and allopatry of species-level adelphotaxa (because of isolation and differentiation in different areas of precinction), although some speciation evidently has occurred within some of the areas of precinction (particularly the Sierra Transvolcanica West and the Talamancan Cordillera).

INTRODUCTION

Prologue

Adults of *Onypterygia hoepfneri* Dejean (Fig. 1) are spectacular beetles: large in size and brilliant green and maroon in color, they excite the aesthetic sensibilities and stimulate the acquisitive instinct of entomologists fortunate enough to locate them. In February 1966, Don Whitehead and I, during the year that we spent together in Mexico, obtained a large series of that species on the lower slopes of the Sierra Madre de Chiapas, to the north of Huixtla, in the state of Chiapas. We made this collection in a stand of oaks growing near the top of a mountain ridge. Concealed in bromeliads attached to the oak trees, the beetles were captured easily by detaching the plants and shaking them over a beating cloth laid on the ground.

Stimulated by the aesthetic appeal of these beetles and the wonder of the environment in which we found them, I think we knew then that *Onypterygia* would be high on the list of taxa for prompt study, following our eventual return to the University of Alberta. For personal reasons, I would have liked to do the revision, but we had agreed previously that the platynines were to be a major focus for Don's contribution to knowledge of the Mexican carabid fauna. In 1967 Don began the work while still a graduate student in Edmonton. He borrowed some supplementary material and, in 1968, studied the types of the species described by those great 19th-century entomologists, P. F. M. A. Dejean, M. de Chaudoir, and H. W. Bates.

Demands resulting from the need to complete his doctoral program interfered with study of *Onypterygia*. Other interruptions followed as the years drifted by. Periodically, I reminded him about this genus, and continued to send him material, including specimens that field parties from my department gathered, specimens sent to me for determination and as gifts, or that I came across in collections of institutions that I visited.

In 1987, Don returned to serious work on *Onypterygia*, and assembled a preliminary draft of a manuscript. The day-to-day requirements of his position in the Systematic Entomology Laboratory plus the time spent generously and willingly in helping others, deflected again the *Onypterygia* project, a deflection that was made permanent by terminal illness and death in May 1990.

I asked for and was granted the opportunity to complete the preparation of the manuscript for publication. Initially, I assumed that the manuscript was sufficiently complete that my task would involve only editorial work and assembly of the plates. A thorough review of the text and prepared figures revealed that much more was required. Because my contribution has been extensive, and because the text is quite different from that which I received, joint authorship seemed appropriate. Authorship confers credit for work done, but equally important, responsibility is established, also.

I am not sure that Don Whitehead would be pleased with the final product, but I am sure he would be relieved to have the task completed. Certainly, I enjoyed the work, for examining the specimens that we had collected brought back happy memories of our time together in the field. From time to time, though, my eyes misted with the thought that our association was a thing of the past. I was for-



Fig. 1.—Habitus, dorsal aspect, of *O. hoepfneri* Dejean. Male, total length 14.1 mm. Guatemala, Zacapa, 3 km SE La Union, 1400–1500 m (UASM).

tunate to have known Donald R. Whitehead and to have enjoyed his friendship for a period that seems all too brief.—George E. Ball

History of Study

The purpose of this paper is to provide a modern taxonomic treatment of the species of *Onypterygia*, as a contribution to the rapidly developing knowledge of

New World Platynini, thanks to the continuing efforts of Liebherr (1986, 1987, 1991a, 1991b, 1992), Moret (1989, 1990a, 1990b, 1993, 1994), and the late Georges Perrault (1990, 1991, 1992). The revision was begun by the senior author in the context of knowledge available at the time (summarized and augmented in part by Whitehead, 1973, 1974), before the individuals noted previously had undertaken their studies, and before Habu's (1978) classification provided a suitable background for genus-level revisions of the tribe Platynini.

Nearly all taxonomic work on *Onypterygia* was published during the 19th century. Although in use as a catalogue name, *Onypterygia* was described and validated first by Dejean (1831), who included three new Mexican species. The concept of the genus has remained essentially unchanged since then, and the name has been applied consistently except for an unjustified emendation as *Onychopterygia* by Agassiz (1847), which was used subsequently by several later authors, including Gemminger and Harold (1868:384), Chaudoir (1878), and Heyne (1895).

Subsequent investigation of Mexican carabid beetles led to description of one new species by Solier (1835:113), three by Chevrolat (1835:158–160), one by Chaudoir (1837:12), one by Castelnau (1840:42), one by Mannerheim (1844:869), and later, two more by Chaudoir (1863:225). These works were summarized by Gemminger and Harold (1868:384), who listed 12 described species.

The first revision of the genus was published by Chaudoir (1878), with description of four additional Mexican species, establishment of junior synonymy for three earlier names, and change to status of variety for another. Bates (1882: 130–133) extended geographical coverage of the genus through description of four new Central American species, as well as presentation of additional locality data for previously described taxa. In a supplement (1884:286–287), he described two additional Mexican species. Heyne (1895:25), evidently unaware of these important papers, validated the Hoepfner specific epithet *dimidiata* for a variety of *O. tricolor*. Casey (1920:224) described as new a species from Guerrero, Mexico. Finally, Ball and Shpeley (1992) described a new species of the genus from Costa Rica.

Casey's publication brought to 24 the total number of validly published species-group names, of which 19 were recognized as species and two as varieties. These names were listed by Csiki (1931:744) and Blackwelder (1944:37), both of whom credited the name *O. dimidiata* to Heyne and Taschenberg, rather than to Chevrolat (1835).

MATERIALS AND METHODS

Materials

This study is based on examination of more than 3000 adults of *Onypterygia*. Additionally, as a basis for comparison, the senior author examined in detail representatives of numerous Neotropical representatives of *Platynus* Bonelli and other platynine genera.

As noted in the Prologue, both authors contributed to the collection of much of the material on which this revision is based. The senior author contributed a manuscript that summarized his studies of type material and the historical background of study of the species, and provided a classification and descriptions of the included taxa, and preliminary phylogenetic and zoogeographic hypotheses for the included taxa. As well, he had prepared many illustrations of structural features. The junior author augmented these contributions by: inclusion of additional material not seen by the senior author; having the SEM figures prepared; adding more line drawings and maps; and assembling the plates.

Some of the additional specimens belonged to species that the senior author had recognized previously, based on single individuals, but declined to name, designating each instead by a lower-case

letter. Such additional specimens justified the senior author's judgment about species recognition. Some of the additional material represented four species (*O. donato* Ball and Whitehead; *O. shpeleyi*, n. sp.; *O. rawlini*, n. sp.; and *O. striblingi*, n. sp.) not seen by the senior author.

Most of the material studied by us is either in the Strickland Museum, Department of Entomology, University of Alberta (UASM), or in the U. S. National Museum of Natural History (USNM, T. L. Erwin, curator). Other collections housing types, or from which material was borrowed, are listed below, along with a four-letter coden used in the text to identify sources of specimens. The names of the respective curators are included, or for private collections, the names of the owners.

ACCS—Achille Casale Collection, Istituto di Zoologia dell' Università di Sassari, via Muroni 25, 07100 Sassari, Italy; AUEM—Entomological Museum, Department of Entomology, Auburn University, Auburn, Alabama 36849, USA (W. E. Clark); BMNH—Department of Entomology, The Natural History Museum, Cromwell Road, London SW7 5BD, United Kingdom (N. E. Stork and M. J. D. Brendell); CASC—Department of Entomology, California Academy of Sciences, Golden Gate Park, San Francisco, California 94118, USA (D. H. Kavanaugh); CDAE—California State Collection of Arthropods, Analysis and Identification Unit, California Department of Food and Agriculture, 1220 N Street, Sacramento, California 95814, USA (F. G. Andrews); CISC—California Insect Survey, Division of Entomology, University of California, Berkeley, California 94720, USA (J. A. Chemsak); CMNC—Entomology Division, Canada Museum of Nature, P. O. Box 3443, Station D, Ottawa, Ontario K1P 6P4, Canada (R. S. Anderson); CMNH—Section of Invertebrate Zoology, Carnegie Museum of Natural History, 4400 Forbes Avenue, Pittsburgh, Pennsylvania 15213-4080, USA (J. E. Rawlins, R. L. Davidson); CNCI—Canadian National Collection of Insects, Biological Resources Division, Centre for Land and Biological Resources Research, Agriculture Canada, K. W. Neatby Building, CEF, Ottawa, Ontario K1A 0C6, Canada. (Y. Bousquet); CUIC—Department of Entomology, Comstock Hall, Cornell University, Ithaca, New York 14853-0999, USA (J. K. Liebherr); FFPC—Foster F. Purington Collection, Department of Entomology, Ohio State University, Columbus, Ohio 43210-1220, USA; FMNH—Field Museum of Natural History, Roosevelt Road at Lake Shore Drive, Chicago, Illinois 60605, USA (H. Dybas, R. L. Wenzel); FSAC—Florida State Collection of Arthropods, Division of Plant Industry, 1911 34th Street S.W., Gainesville, Florida 32602, USA (M. C. Thomas); INBC—Instituto Nacional de Biodiversidad, Apto. 22-3100, Santo Domingo de Heredia, 3100, Heredia, Costa Rica (Angel Solís); JEWG—J. E. Wappes Collection, J. E. Wappes, 5336 Fallen Oak, Oak Village North, Bulverde, Texas 78163, USA; MCPM—Milwaukee City Public Museum, 800 W. Wells Street, Milwaukee, Wisconsin 53233, USA (G. R. Noonan); MCZC—Department of Entomology, Museum of Comparative Zoology, Harvard University, 26 Oxford Street, Cambridge, Massachusetts 02138, USA (D. G. Furth); MNHP—Entomologie, Muséum National d'Histoire Naturelle, Paris 75005, France (T. Deuve); MSUC—Department of Entomology Collection, Michigan State University, East Lansing, Michigan 48824-1115, USA (F. W. Stehr); OXUM—Hope Entomological Collections, University Museum, Parks Road, Oxford OX1 3PW, United Kingdom (G. McGavin); RHTC—Robert H. Turnbow Collection, R. H. Turnbow, Jr., Directorate of Engineering and Housing, Building 1404, Fort Rucker, Alabama 36362-5137, USA; SEMC—Snow Entomological Museum, University of Kansas, Lawrence, Kansas 66044, USA (J. S. Ashe); TAMU—Department of Entomology Insect Collection, Department of Entomology, Texas A & M University, College Station, Texas 77843, USA (H. R. Burke); UCDC—The Bohart Museum of Entomology, University of California, Davis, California 95616, USA (R. M. Bohart); UMMZ—Museum of Zoology, University of Michigan, Ann Arbor, Michigan 48109-1079, USA (M. F. O'Brien); UNAM—Colección Entomología, Instituto Biología, Universidad Nacional Autónoma de México, Apartado Postal 70133, 04510 México D. F. (M. and C. Santiago Zaragoza); UNAN—Entomological Collection, Escuela de Biología, Facultad de Ciencias, Universidad Nacional Autónoma de Nicaragua, Leon, Nicaragua (J. M. Maes); ZSMC—Zoologische Staatssammlung, Munchhausenstraße 21, D-81247, München, Germany (M. Baehr; G. Scherrer).

Holotypes and allotypes of newly described taxa have been deposited in the U. S. National Museum of Natural History, or returned to the appropriate lending institutions.

Methods

Taxonomic Conventions

Taxonomic principles, criteria for ranking groups of specimens as species, and general working methods are standard, and have been explained previously (see, for example, Ball and Negre, 1972, and Whitehead, 1972). The senior author chose not to use the subspecies category, in the spirit that it is much more important to recognize how geographically differentiated organisms fit together than it is to distinguish them nomenclaturally. However, subspecies names are used as a convenient informal notation to discuss geographical variation in the species *O. fulgens* and *O. tricolor*.

We use only one informal category (species group) between genus and species. For the present, this seems adequate to express our understanding of the evolutionary structure of the genus.

Phylogenetic Considerations

The species groups are based on a combination of more or less distinctive features, and each group is postulated as monophyletic. Within species groups, close phylogenetic relations are postulated for allopatric or parapatric species pairs, where marked similarities in distinctive features seem decisive.

Species groups are in the sequence that reflect the views of the senior author about degree of primitiveness, beginning with the *famini* group, and ending with the *fulgens* complex of the *fulgens* group.

Terms for phylogenetic analysis are standard, except for "adelphotaxon." This word was introduced by Ax (1987:36) as a substitute for "sister taxon." The advantage of using adelphotaxon is that, being of classical origin, it will be the same in all European languages.

Taxonomic Treatments of Species

These include the standard elements of: synonymy; a diagnosis; figures of male genitalia for most species; a brief description of each species, including measurements; notes about habitat and plant community occupied, as inferred from collecting data; and a statement about geographical range, which is amplified by a range map for each species. Additionally, we include statements about chorological affinities (stated in terms of range overlap with other species of the genus, particularly close relatives), and postulated phylogenetic relationships. The latter two aspects are as much properties of a species as are its structural features, and should be included, therefore, in a taxonomic treatment.

Measurements

These were used to indicate size and proportions. The following measurements were made, using an ocular micrometer in a Wild S5 Stereobinocular Microscope, at a magnification of 25 \times : length of head—linear distance from anterolateral angle of clypeus to posterior margin of left eye (if the left side was damaged, the measurement was taken on the right side); length of pronotum—linear distance from anterior (apical) to posterior (basal) margin, measured along the midline; width of pronotum—greatest linear transverse distance, measured at right angle to the midline; width of pronotum at base—linear distance between posterolateral angles; length of elytra—linear distance from basal ridge to apex of one elytron, along the suture; width of elytra—greatest linear transverse distance across both elytra, measured at right angle to suture.

These measurements were added or combined in ratios, and designated as follows: TL—body length (sum of length of head, pronotum, and elytra); PL/PW—length of pronotum/width of pronotum; WP/WH—maximum width of pronotum/width of head; LP/WP—length of pronotum/maximum width of pronotum; WP/WPb—maximum width of pronotum/width of pronotum at base; and LE/WE—length of elytra/width of elytra.

In the descriptions, qualitative terms are offered to designate three classes, and thus to generalize the numerical values: for size (TL), small, intermediate, and large; for ratios, low, intermediate, and high. Each class represents approximately a third of the measured range of variation of each measurement and ratio.

Dissections and Illustrations

Dissections were made using standard techniques. Genitalia and other small structures were preserved in glycerine, in microvials, pinned beneath the specimens from which the sclerites had been removed. Hind wings, and sclerites that had been gold-coated for study with the scanning electron microscope were glued to cards and pinned beneath the specimens from which they had been removed.

A Cambridge S-250 scanning electron microscope was used to examine and photograph gold-coated sclerites. Line drawings were prepared by using a camera lucida (drawing tube) attached to a Wild S5 stereobinocular microscope.

Descriptions

Descriptive statements are consolidated to reduce redundancy: those statements that apply to all species of *Onypterygia* are in the generic description, and are not repeated elsewhere; distinctive character states of all species of a group are in the group treatment; and character states confined to individual species appear in the specific descriptions. The disadvantage to this method of presentation is that, to obtain a full description of a species, one must read the three descriptions: specific, species group, and generic.

Type Material

For type specimens (holotypes, lectotypes, allotypes, and paratypes), label data are reproduced as exactly as possible, short of photographic images. This includes information about label shape (if other than square or rectangular), color of paper (other than white), color of ink (other than black), and nature of script (handwriting, rather than printing). Words referring to these properties are placed in square brackets to distinguish them from the text of the labels. Each label begins and ends with quotation marks; line endings are indicated by slash marks (/).

Catalogue Citations of Species

Catalogue entries noted in the synonymy of the genus *Onypterygia* (Csiki, 1931:743–744; Blackwelder, 1944:47) are not repeated in the species' synonymies.

Terms for Structural Features

Most of the words we used to designate details of structures are found in entomology textbooks or are used by coleopterists, generally. Other words, required to designate particular structures or parts thereof, are not in general use, although they have been used by the junior author in several publications (e.g., Shpeley and Ball, 1994). We provide information about these words here. Also, we draw attention to some special features of adults useful in species recognition.

Body Parts.—The term "segment" is restricted to those body parts that reflect embryonic somites; thus, somite-like portions of the abdomen are referred to as segments.

Abdominal segments are designated by Roman numerals, corresponding to the respective somites. The first complete sternum is III, and the last one normally exposed is VII. For numbering of the genital segments, we follow Bills (1976).

Portions of limbs are designated by the suffix "-mere," the prefix depending upon the limb in question: antenno-, palpo-, tarso-, etc.

Microsculpture.—A sculpticell is the space enclosed on the surface of the cuticle by adjacent microlines of the integumental system of microsculpture (Allen and Ball, 1980:486). Surface sculpture of the elytra provides some taxonomically useful features (Fig. 2–5). For most species, microlines are very fine; the transverse lines persist, while most of the longitudinally-oriented lines are absent, or almost so (Fig. 2, 4A, 5A), except in foveae (Fig. 4C, 5C). For *O. hoepfneri*, both transverse and longitudinally directed lines are about equally distinct.

Mesh pattern ranges from nearly isodiametric (mesh length/width ca. 1.00; Fig. 2) to slightly transverse (mesh L/W more than 1.00; Fig. 3). Table 1 summarizes measurements and shows that mesh size and shape are not correlated simply with size of elytra. For example, the *O. wappesi* specimen is substantially smaller than the specimen of *O. hoepfneri*, but the meshes of the former are longer than the meshes of the latter. Also, the elytra of *O. iris* Chaudoir and of *O. hoepfneri* are the same size, but the meshes of the former are wider than the meshes of the latter.

Macrosculpture and Punctures.—The integument of adults of most species of *Onypterygia* is smooth overall. Some species have a preapical lateral swelling on each elytron (a callus; Fig. 11B: pc). Foveae are evident on the elytral disc and apical declivity of two species (Fig. 5B, 43).

Antennae.—In descriptions of color, two parts are referred to: basal (antennomeres 1–4), and apical (antennomeres 5–11).

Labium.—The word "ligula" is used for glossae + paraglossae. In turn, the fused, sclerotized glossae characteristic of beetles are termed the glossal sclerite (Ball and Shpeley, 1983:746).

Elytra.—Longitudinal grooves on the dorsal surface ("striae" of most authors) are designated as interneurs (Erwin, 1974:3–5). For a different perspective on the use of this term, see Cooper (1990).

Tarsi.—The term climbing setae is used by Stork (1980:177) to designate "normal adhesive setae." Located on the ventral surfaces of tarsomeres 1–4, these setae are of the "simple type" exhibiting few morphological adaptations for adhesion (Stork, 1980:305). In *Onypterygia* adults (Fig. 11D:cs), as in adults of *Demetrias atricapillus* Linnaeus (Stork, 1980:195), the climbing setae are round in cross section, but slightly flattened dorsoventrally, and curved proximally preapically.

Male Genitalia.—In form and range of variation of the male genitalia (median lobe, parameres, and internal sac), *Onypterygia* does not differ much from the related genus, *Platynus* (cf. Liebherr, 1987: 318, fig. 57; 339, fig. 75–77; 349, fig. 84–88). The internal sac exhibits striking modification, from asetose to setose, with fields of setiform spines (Fig. 25C, D), or much of the ventral surface with short setiform spines. Spinose sclerites (Fig. 44D:Sc1, Sc2) and lobes with microtrichia basally and apically (Fig. 48, 80) characterize many species.

Ovipositor.—Ball and Shpeley (1983:746) explain terms used for sclerites and setae, and for orientation of sclerites. Note that for stylomeres, the surfaces that are ventral in the infolded or retracted position are lateral in the extended position; such surfaces are designated as lateral.

Stylomere 2 (Fig. 12–16) of *Onypterygia* females provides useful diagnostic features, the most

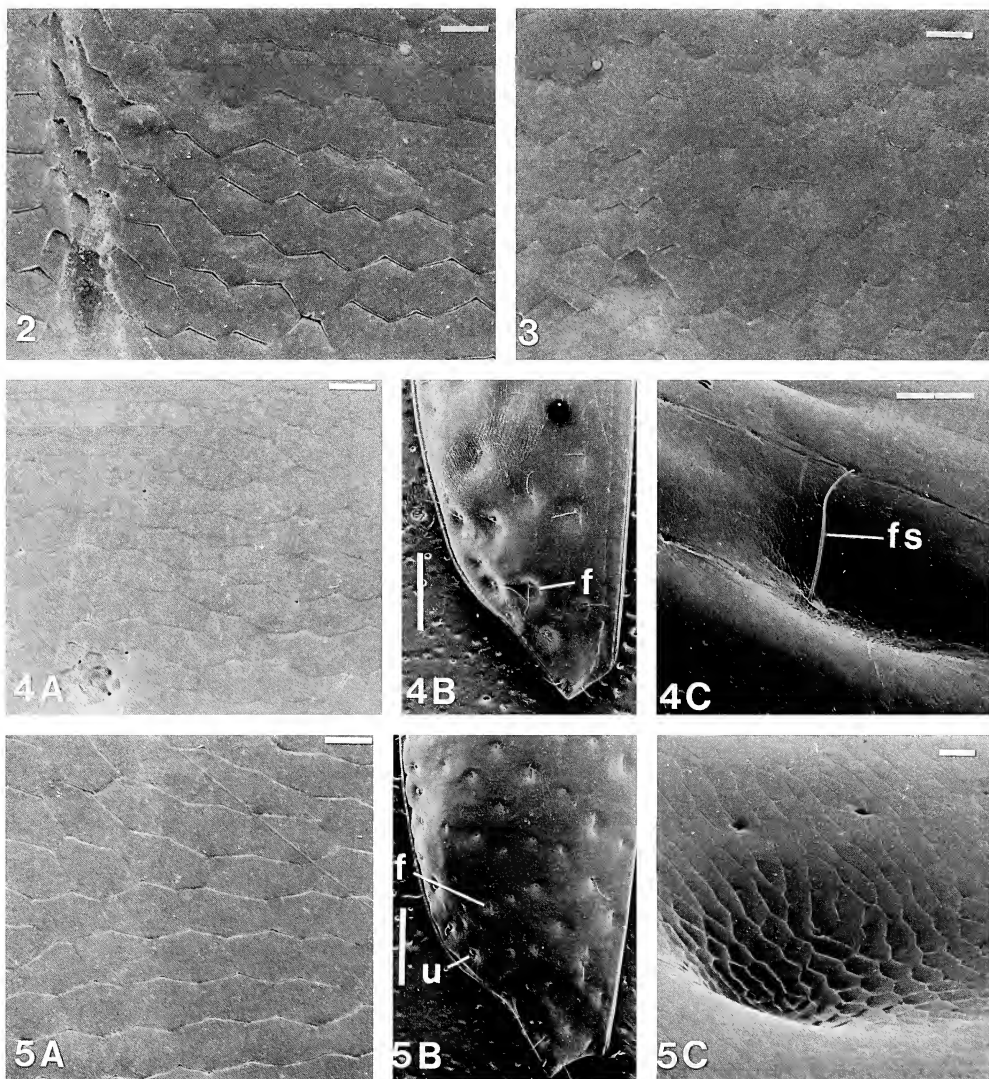


Fig. 2-5.—SEM photographs of dorsal surfaces of elytra. Fig. 2, 3. Microsculpture of elytral disc, in basal third, interval 3, of: 2, *O. famini* Solier; 3, *O. hoepfneri* Dejean. Fig. 4, 5. Elytra: A—microsculpture of elytral disc, in basal third, interval 3; B—apical portion of elytron, showing foveate punctures on disc and apical declivity; and C—foveate punctures, enlarged, of: 4, *O. polytreta*, n. sp.; and 5, *O. crabilli*, n. sp. Legend: f—foveate puncture, fs—seta in foveate puncture, u—umbilicate puncture. Scale bars: for Fig. 2-4A, 5A, 5C = 10 μ m, for Fig. 4C = 100 μ m; for Fig. 4B, 5B = 1.0 mm.

striking being the dense pad of ensiform setae on the lateral surface (Fig. 16A; cf. Fig. 12A:es) that characterizes some species.

TAXONOMIC ACCOUNTS

Genus *Onypterygia* Dejean

Onypterygia Dejean, 1831:346. Species originally included: *O. fulgens* Dejean, *O. hoepfneri* Dejean, and *O. tricolor* Dejean. Type species: *O. fulgens* Dejean (designated by Hope, 1838:72); Castel-

Table 1.—Measurements and proportions of microsculpture mesh of a sample of *Onypterygia* adults.

Species	Sculpticell L/W		Sculpticell width (μ)		Elytron width (mm)
	Range	Mean	Range	Mean	
<i>O. wappesi</i>	0.78–0.94	0.84	13.60–15.30	13.94	1.99
<i>O. shpeleyi</i>	0.25–0.35	0.30	20.00–23.00	21.40	1.60
<i>O. famini</i>	0.80–1.00	0.90	13.60–17.00	15.30	2.08
<i>O. iris</i>	0.70–1.00	0.94	13.60–17.00	14.45	3.15
<i>O. polytreta</i>	0.57–0.70	0.61	15.30–18.70	17.34	2.90
<i>O. crabilli</i>	0.54–0.70	0.66	17.00–20.40	18.02	2.74
<i>O. hoepfneri</i>	1.38–1.92	1.59	10.20–11.90	10.88	3.15

nau, 1840:41; Chevrolat, 1847:117; Chenu and Desmarest, 1851:135; Lacordaire, 1854:358; Bates, 1882:130; Casey, 1920:224; Csiki, 1931:743; Blackwelder, 1944:37; Whitehead, 1973:175; Whitehead and Ball, 1975:595; Erwin et al., 1977:4.31; Reichardt, 1977:413; Liebherr, 1986:22, 86; Ball and Shpeley, 1992:403; Liebherr, 1992:6.
Onychopterygia Agassiz, 1847:260 (unjustified emendation). Gemminger and Harold, 1868:384; Chaudoir, 1878 (1879):275.

Generic Name

Onypterygia is based on two Greek words: *onyx*, claw; and *pterygion*, little wing, or feathers. Together, the words would seem to mean “feathered claws,” in allusion to the strikingly developed pectinations on the claws of adults of this genus (Fig. 11E–H).

Diagnostic Combination

With character states of subtribe Platynina (Habu, 1978:4), and tarsomere 4 of fore tarsus asymmetrically lobate apically (Fig. 11C:l-4) tarsal claws pectinate, pectinations curved ventromesally, long (Fig. 11E–H), head slightly constricted behind eyes and across occiput, and median lobe of male genitalia pale in color, not melanistic. The long, curved pectinations of the tarsal claws are virtually sufficient in themselves to distinguish *Onypterygia* adults from those of other platynine genera.

Description

With character states of subtribe Platynina. Habitus (Fig. 1, 17–20) slender, body terete, elytra elongate. Length (TL) ca. 5–18 mm, width ca. 2–7 mm. Range of values in Table 2 for following ratios: WP/WH, LP/WP, WP/WPb, and LE/WE.

Color.—Body and elytra rufous to blue, maroon, and green, alone or in combination. Antennae, mouthparts, and legs piceous to rufotestaceous.

Microsculpture.—Ventral surface with mesh pattern generally transverse. Head dorsally with mi-

Table 2.—Range of variation in measurements (mm) and values for selected ratios for species groups of the genus *Onypterygia* Dejean.

Species group	TL (mm)	WE (mm)	WP/WH	LP/WP	WP/WPb	LE/WE
<i>perissostigma</i>	8.2	2.5	1.04	1.16	1.16	1.96
<i>wappesi</i>	5.4–8.0	2.2–3.5	1.41–1.56	0.78–0.88	1.20–1.40	1.42–1.55
<i>aeneipennis</i>	6.7–8.7	2.7–3.3	1.28–1.39	0.84–0.91	1.22–1.28	1.47–1.60
<i>famini</i>	9.0–11.5	3.4–4.4	1.31–1.38	0.90–0.92	1.17–1.20	1.53–1.65
<i>pusilla</i>	7.0–9.0	2.7–2.9	1.33	1.18	1.29	2.00
<i>angustata</i>	7.5–11.3	3.0–4.0	1.33–1.56	0.84–1.00	1.18–1.25	1.73–1.77
<i>fulgens</i>	10.4–17.5	3.8–6.4	1.16–1.55	0.75–1.16	1.19–1.47	1.70–2.05

croclines distinctly impressed to absent (surface smooth), mesh pattern isodiametric to slightly transverse. Labrum with mesh pattern isodiametric to slightly transverse in places, microlines distinctly impressed, sculpticells slightly convex. Pronotum with microlines distinctly impressed to evanescent to absent (surface smooth); mesh pattern transverse. Elytra (Fig. 2, 3, 4A, 5A) with microlines distinctly impressed to evanescent to absent in part or entirely (surface smooth); mesh pattern isodiametric (Fig. 2) to transverse (slightly, Fig. 4A, 5A; and markedly), to slightly elongate (Fig. 3).

Luster.—Surface dull to shining, to slightly iridescent.

Macrosculpture.—Surface generally smooth. Head with shallow frontal impressions, linear or in form of irregular basins. Vertex between eyes without or with distinct ridge each side. Elytra smooth except more or less impressed interneurs, or with prominent foveae (Fig. 4B, C; 5B, C; 20); or with more or less distinctly developed lateral preapical callus (Fig. 11B:pc). Abdominal sterna II–VII laterally with surface irregularly sculptured by depressions of various sizes.

Chaetotaxy (Fixed Setae).—Array standard for Platynina, with exceptions: medial pair of lateral setae of pronotum present or absent; each elytron with three or two discal setae (anterior seta present or absent). Setal formula of legs as follows (numbers in sequence fore, mid, hind): coxae (0–2–2); trochanters (1–1–1); femora, ventrad (2–2–2 or 2–2–3), dorsally (ca. 10–ca. 10–0 to 2). Tarsomere 5 (Fig. 11D, G:vs) with row of setae on each ventrolateral margin. Abdominal sterna IV–VI each with single pair or more of ambulatory setae. Abdominal sternum VII with setae near posterior margin: one or two pairs in males, two to seven pairs (14 setae) in females.

Head.—Average for Platynina: clypeus rectangular, transverse. Occiput behind eyes slightly constricted, marked dorsally by shallow transverse depression. Eyes slightly flattened to markedly convex, prominent. Antennae average for Platynina: antennomeres 1–3 with few apical setae; antennomeres 4–11 with dense vestiture of short and varied sense organs; antennomeres slender, longer than wide.

Mouthparts.—Average for Platynina. Mandibles as in Fig. 6A–F. (See Acorn and Ball, 1991, for explanation of structural details.) Palpomeres with terminal articles slender, elongate. Mentum with prominent tooth.

Prothorax.—Pronotum transverse (Fig. 21, 22) to longer than wide (Fig. 47), dorsal surface slightly convex. Anterior and posterior margin each with groove more or less clearly developed, and thus more or less clearly beaded; lateral margins beaded partially or completely, or not beaded. Median longitudinal impression distinct but shallow; anterior transverse impression distinct to evanescent; posterolateral impressions basin-like to linear, co-extensive or not with lateral marginal grooves. Anterior (or apical) margin straight (Fig. 47) to slightly concave (Fig. 39, 54A); lateral margins rounded, evenly so posteriorly (Fig. 28, 73) or sinuate (Fig. 21, 22, 38); posterior (or basal) margin straight (Fig. 21, 53), slightly convex (Fig. 22, 69), or markedly convex (Fig. 30B), sinuate laterally (Fig. 67). Anterolateral angles narrowly rounded, projected forward slightly, or not. Posterolateral angles acute (Fig. 21), rectangular (Fig. 22), to broadly rounded (Fig. 28, 73). Prosternum with apex of intercoxal projection rounded or truncate.

Pterothorax.—Average for Platynina: metathorax of normal proportions, with metepisterna longer than wide at base; or short, with anterior and lateral margins nearly equal, i.e., metepisternum about as long as wide.

Elytra.—Elongate, each elytron from about 1.5 to about twice as long as wide; humeri fully developed and broadly rounded, or obliquely narrowed; lateral margins straight, slightly sinuate medially or broadly rounded, and narrowed and more or less sinuate preapically (Fig. 4B, 5B, 7, 8); apex rounded (Fig. 7, 8), or projected as spine of varying length (Fig. 4B, [denticulate], 5B, 10 [acuminate, spine short], 11A:ae [acuminate, spine long]); apex of suture rounded or variously denticulate and projected (Fig. 8:se). Basal groove and ridge distinct, complete. Intervals flat; interneurs variously developed, from all interneurs impressed equally throughout their length (Fig. 7, 8) to only interneur 1 distinctly impressed, others much shallower, especially on apical declivity Fig. 10:11, 12; 11A); parascutellar interneur separate from interneur 1.

Hind Wings.—Macropterous or brachypterous, or dimorphic. Fully developed wings with oblongum and wedge cells (Fig. 23, 78, 79:o, w) complete.

Legs.—Long and slender. Mid- and hind tibiae each with three rows of spines, dorsal (or posterior) surface not spined. Hind tarsomeres 1–3 each bisulcate or not; tarsomere 4 bilobed (Fig. 11C:1–4), lobes slightly asymmetric, ventrally moderately (Fig. 11C) to densely (Fig. 11F) setose or ciliate. Setae of climbing type. Claws virtually “chelate” (see Liebherr, 1986:26) with long pectinations (Fig. 11D–H:p) curved ventromesally. Males with biseriate adhesive vestiture on fore tarsomeres 1–4 (cf. Stork, 1980:190, fig. 9E–H; 10A–C; 17C, D).

Abdomen—Pregenital Segments.—Sterna II–VII average for Platynina (macrosculpture and chaetotaxy noted above).

Male Genitalia.—Median lobe slender, elongate, in lateral aspect curved ventrad (Fig. 32A, 59A); anopic (i.e., membranous portion dorsal, and extended about half length of median lobe); apical portion

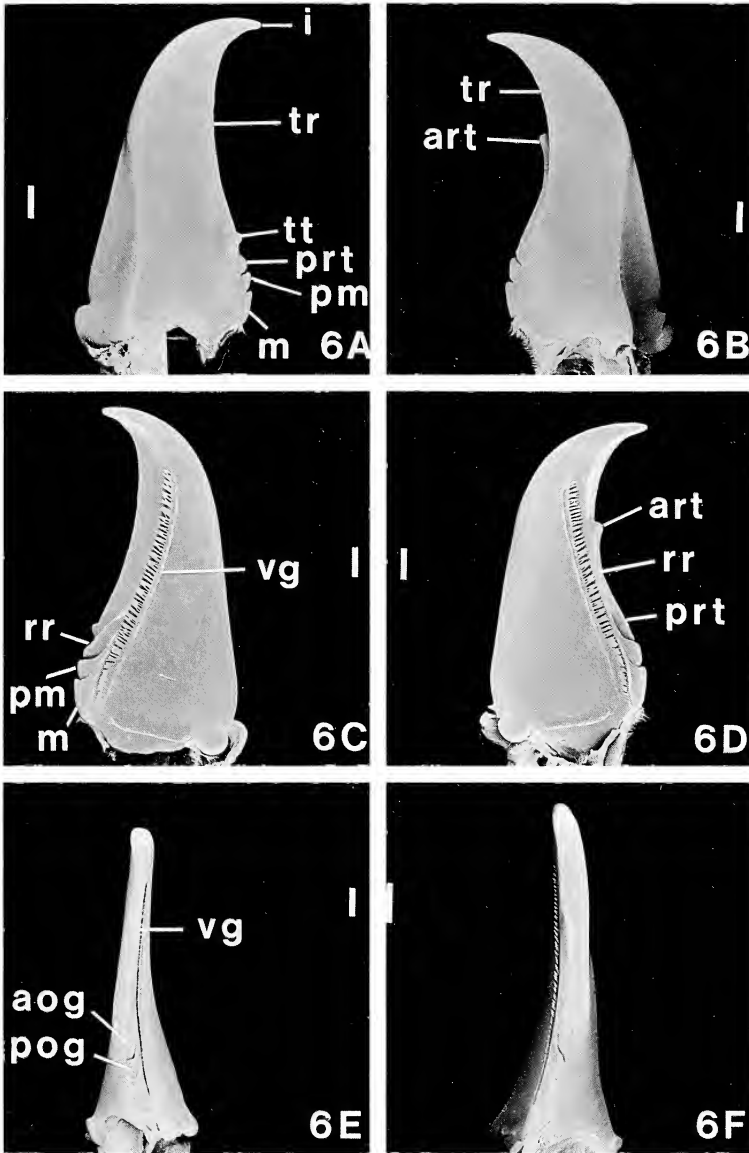


Fig. 6.—SEM photographs of mandibles of *O. famini* Solier. A, C, E. Left mandible: dorsal, ventral, and occlusal aspects, respectively. B, D, F. Right mandible: dorsal, ventral, and occlusal aspects, respectively. Legend: aog—anterior occlusal groove, art—anterior retinacular tooth, i—incisor tooth, m—molar tooth, pm—premolar tooth, pog—posterior occlusal groove, prt—posterior retinacular tooth, rr—retinacular ridge, tr—terebral ridge, tt—terebral tooth, vg—ventral groove. Scale bars = 100 μ m.

very short (Fig. 44C, D), to moderately long (Fig. 89); in dorsal aspect, apex acute (Fig. 44A) to more broadly rounded (Fig. 56A), to spatulate (Fig. 82A). Parameres (Fig. 59A) average for Platynina, left larger than right, both quite broad, paddle-like, each with apex broadly rounded, asetose.

Internal sac short (Fig. 32A) or markedly elongate (Fig. 97A, B), with or without basal and preapical lobes. Armature microtrichial patches, or patches of spinose sclerites (Fig. 44D:Sc1, Sc2), or of setose spines (Fig. 25C, D:s.sp; 82C), or generally covered with short setose spines (Fig. 31C).

Ovipositor.—Valvifers average for Platynina. Stylomere 1 with row of setae preapically. Stylomere

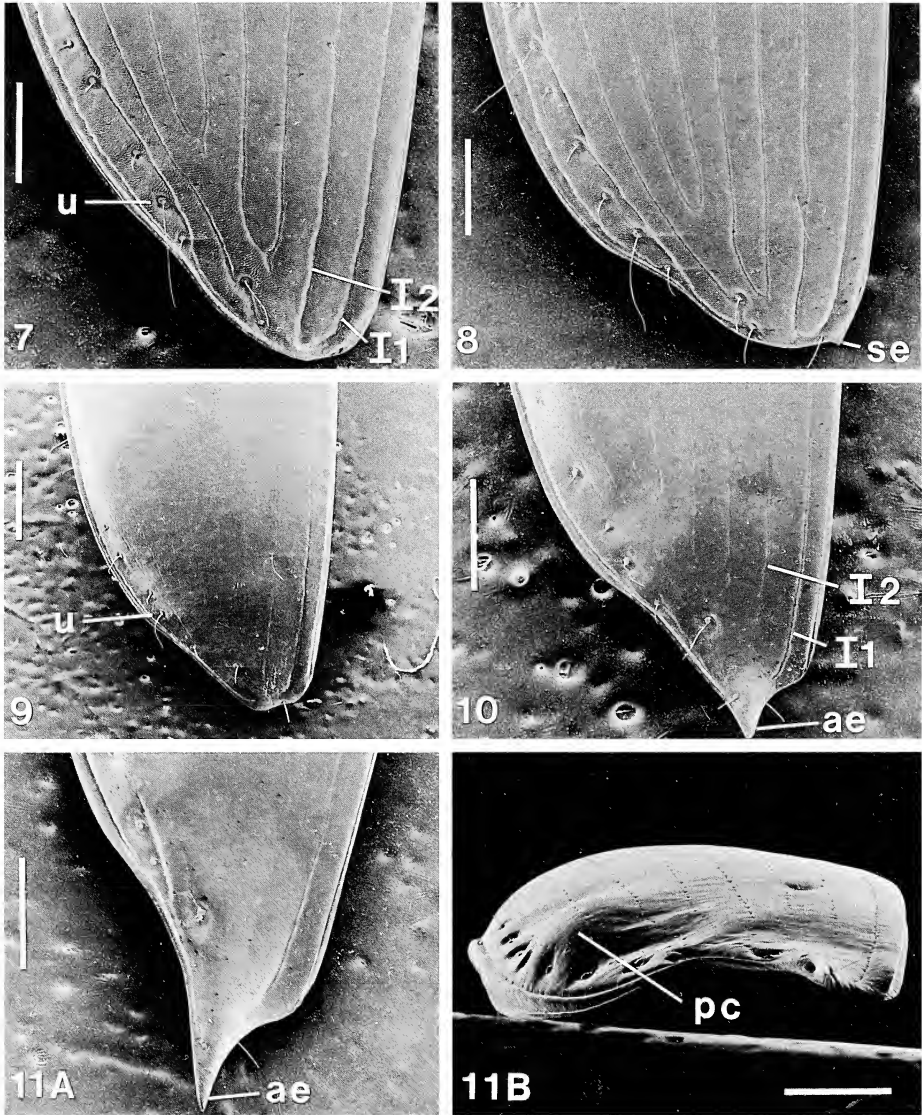


Fig. 7-11B.—Left elytron, apical portion, dorsal aspect, of: 7, *O. famini* Solier; 8, *O. wappesi*, n. sp.; 9, *O. hoepfneri* Dejean; 10, *O. longispinis* Bates; 11A, *O. kathleenae*, n. sp.; 11B, left elytron, posterodorsal aspect of *O. kathleenae*, n. sp. Legend: ae—apical spine of elytron, I1—interneur 1 or sutural interneur, I2—interneur 2, pc—preapical callus, se—sutural denticle of elytron, u—umbilical puncture. Scale bars: for Fig. 7, 8, 10, 11A, 11B = 500 μ m; for Fig. 9 = 1.0 mm.

2 with standard array of setae (Fig. 12-16:s2): lateral and medial ensiform setae (es, mes), pair of nematiform setae ventrally (ns) and six to ten pegs in sensory groove (sg). Three forms, as follows: form 1, ventral surface narrow, dorsal surface markedly curved, with lateral ensiform setae more or less marginal, and with single medial ensiform seta (Fig. 12A, B; 14); form 2, broad, dorsal surface less curved, ensiform setae numerous, remote from dorsal margin, and medial ensiform seta present (Fig. 15A, B); and form 3 as in form 2, but broader, lateral ensiform setae remote from dorsal margin, clustered as pad, and medial ensiform seta absent (Fig. 16A, B).

Internal Female Genitalia.—Investigated in two species only. For *O. famini*, bursa copulatrix bul-

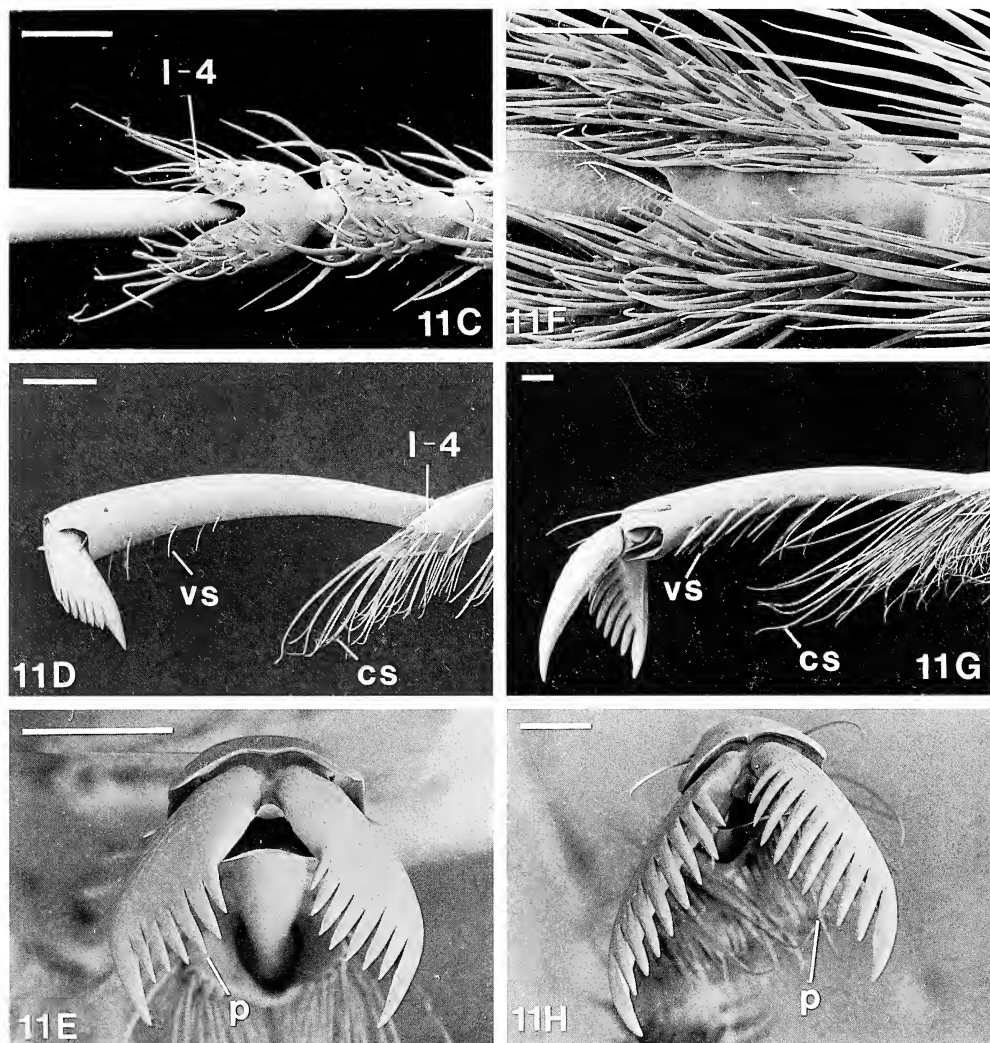


Fig. 11C-H.—SEM photographs of left hind tarsomeres of *Onypterygia* species. C–E, *O. perisostigma*, n. sp.: C, apical portion of 2, 3, and 4, and basal portion of 5, ventral aspect, 3 and 4 with climbing setae in lateral rows; D, apical portion of 4, with climbing setae ventrally, and 5, with claws and ventrolateral setae, lateral aspect, 4, with climbing setae ventrally; E, claws, terminal aspect. F–H, *O. fulgens* Dejean: F, apical portion of 3, 4, and basal portion of 5, 3 and 4 with climbing setae in dense lateral rows; G, apical portion of 4, with ventral climbing setae, and 5, with claws and ventrolateral setae, lateral aspect; H, tarsal claws, terminal aspect. Legend: cs—climbing seta, l-4—terminal lobe of tarsomere 4, p—pecten of tarsal claw, vs—ventrolateral seta of tarsomere 5. Scale bars = 100 μ m.

bous, about as wide as long, and basal half slightly sclerotized; spermatheca digitate, short, annular, on short duct; spermathecal gland duct inserted at base of spermatheca, with large apical bulb constricted at base.

For *O. fulgens*, bursa copulatrix ca. four times longer than wide, folded, accordion-like, with surface sclerotization confined to base; spermatheca and spermathecal gland as described for *O. famini*, above (cf. Liebherr, 1986:13, fig. 5C, *O. tricolor* Dejean).

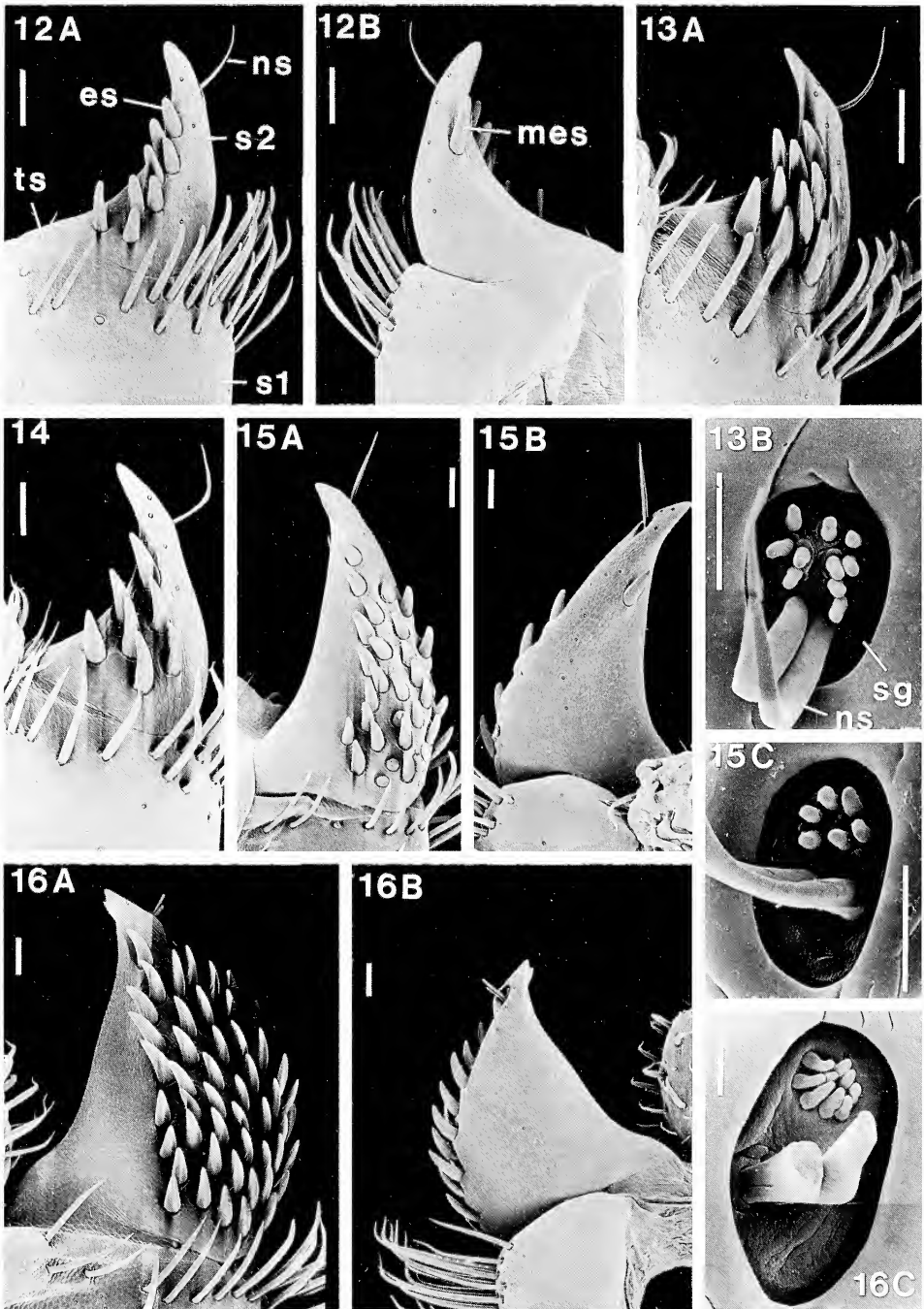


Fig. 12-16.—SEM photographs of left stylomeres of ovipositors of *Onypterygia* species. Fig. 12, stylomere 2 and apical portion of stylomere 1, of *O. wappesi*, n. sp.: A, lateral aspect; B, medial aspect. Fig. 13, stylomere 2 and apical portion of stylomere 1 of *O. batesi*, n. sp.: A, left lateral aspect; B, ventral aspect, showing sensory furrow with two nematiform setae and ten sensory furrow pegs. Fig. 14, stylomere 2 and apical portion of stylomere 1, lateral aspect, of *O. cupricauda* Casey. Fig.

Geographical Distribution

The range of *Onypterygia* extends from Nearctic northern Mexico through Neotropical Middle America to northern South America.

Way of Life

Adults of most species of *Onypterygia* are arboreal, collected commonly by beating vegetation (both trees and shrubs, and leaf litter that accumulates in tangles of vines and branches of standing plants), although some have also been found on the ground. They fly readily during the day, when disturbed. Many specimens have been collected at night, principally by ultraviolet light traps; thus, they seem to be night-active. During the dry season, especially January through April, apparently they become inactive, but may be found in abundance in the leaf axils of arboreal bromeliads. The genus is forest-inhabiting, ranging from rather dry lowland woodlands to middle montane cloud forests. Characteristic of moderate altitudes in Middle American forests, *Onypterygia* tends to be replaced ecologically by various Lebiini in the lowlands, and to be limited in uplands by the occurrence there of colder, drier circumstances. Because of these limiting factors, many species are quite widespread, yet exhibit complex patterns of geographical variation.

Relationships

Dejean (1831:277–279) placed *Onypterygia* in the Truncatipennes (second subtribe, characterized by lack of a constricted head), near the lebiine genera *Demetrius* and *Dromius*, on the basis of: body more or less elongate and palpi not securiform; then, separated from the other two genera by claws of the tarsi with very pronounced denticles. Dejean noted the resemblance between *Dyscolus* and *Onypterygia*, and further with additional platynine genera: *Dolichus*, *Platynus*, and *Anchomenus*. He suggested that *Onypterygia* may be intermediate between the Feroniens (to which the above-noted genera belonged) and the Truncatipennes. Hope (1838:73) suggested that *Onypterygia* should be placed in a distinct “family” (i.e., tribe). Castelnau (1840:41), following Dejean, included *Onypterygia* in the tribal group Lebiites, one of the major truncatipennian elements.

Chenu and Desmarest (1851) placed *Onypterygia* in the tribe Simplicimanes (second division, Calathides), on the basis of the pectinate tarsal claws, and other platynine features. Lacordaire (1854:358) placed *Onypterygia* in “Tribu XXXV, Anchomenides,” the approximate equivalent of the modern group Platynini. He noted the truncatipennian affinities that concerned his predecessors, but the close overall resemblance between *Onypterygia* and the genus *Dyscolus*, concluding that the former genus formed a transition between the Truncatipennes and the Anchomenini. Chaudoir (1878) did not comment about relationships of *Onypterygia*, but treated it in the same work with the platynine genera *Dicranoncus* Chaudoir and *Colpodes* MacLeay. Subsequent authors have included *Onypterygia*

←

15, stylomere 2 and apical portion of stylomere 1, of *O. exeuros*, n. sp.: A, lateral aspect; B, medial aspect; C, ventral aspect, showing sensory furrow with two nematiform setae and six sensory furrow pegs. Fig. 16, stylomere 2 and apical portion of stylomere 1, of *O. sallei* Chaudoir: A, lateral aspect; B, medial aspect; C, ventral aspect, showing sensory furrow with bases of two nematiform setae and nine sensory furrow pegs. Legend: es—ensiform seta, mes—medial ensiform seta, ns—nematiform seta, ts—trichoid seta, S1—stylomere 1, S2—stylomere 2, sg—sensory furrow, sgp—sensory furrow peg. Scale bars: for Fig. 13A, 15C, 16C = 10 μ m; for Fig. 12A–13A, 14–15B, 16A–16B = 50 μ m.

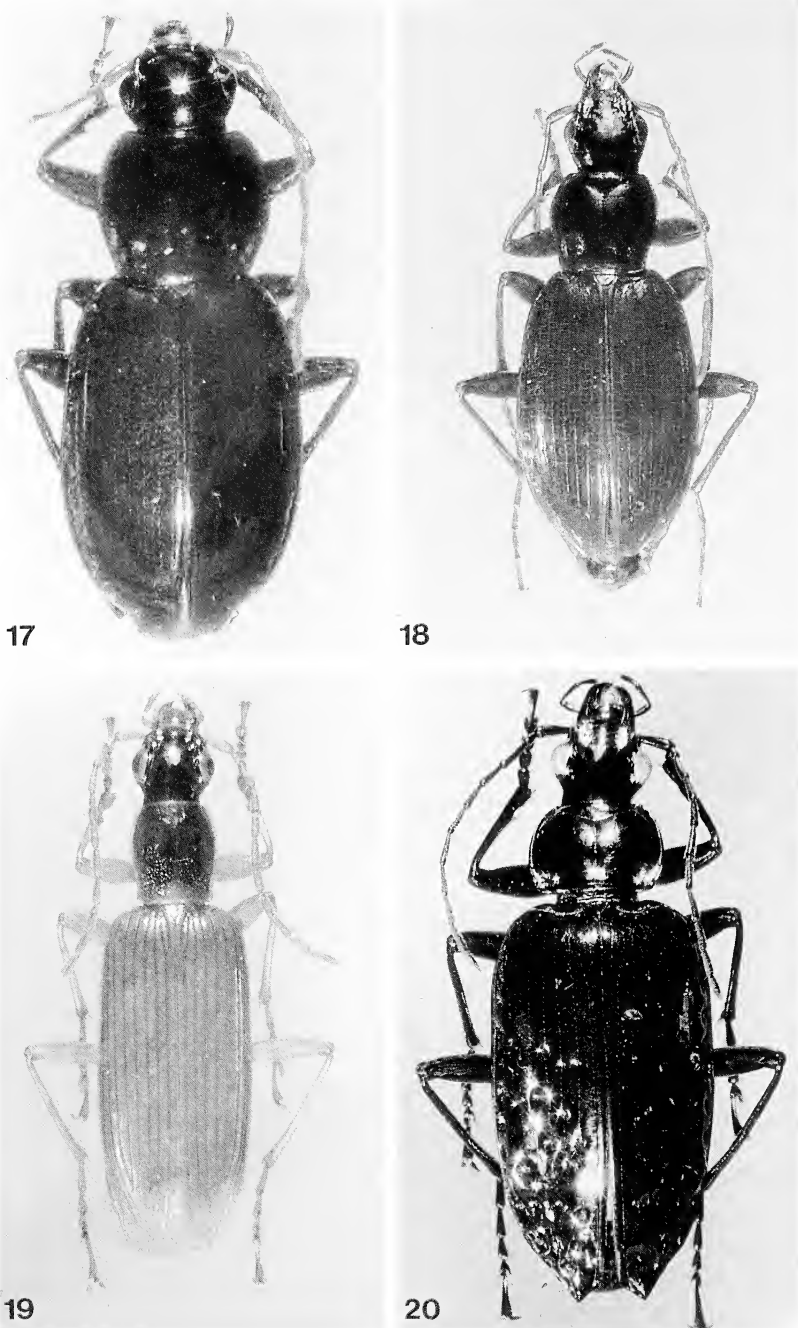


Fig. 17–20.—Photographs of habitus of representative species of *Onypterygia* species. Fig. 17, *O. pacifica*, n. sp. Holotype, male, TL = 6.7 mm. MEXICO, Oaxaca, 3.2 km. N San Jose del Pacifico (TAMU). Fig. 18, *O. stenapteryx*, n. sp. Holotype male, TL = 6.7 mm. MEXICO, Michoacan, 30.2 km. W. Uruapan (USNM). Fig. 19, *O. perissostigma*, n. sp. Paratype, male, TL = 7.4 mm. Mexico, Oaxaca, 27.2 km. S. Valle Nacional (USNM). Fig. 20, *O. polytreta*, n. sp. Paratype male, TL = 13.1 mm. PANAMA, Chiriqui, Pr. Cerro Pando (USNM).

Table 3.—Checklist of the species groups and species of *Onypterygia* Dejean.

<i>O. famini</i> species group	<i>O. angustata</i> species group
<i>O. famini</i> Solier	<i>O. longispinis</i> Bates
<i>O. cyanea</i> Chaudoir	<i>O. angustata</i> Chevrolat
<i>O. wappesi</i> species group	<i>O. pseudangustata</i> , new species
<i>O. wappesi</i> , new species	<i>O. striblingi</i> , new species
<i>O. amecameca</i> , new species	<i>O. fulgens</i> species group
<i>O. atoyac</i> , new species	<i>O. iris</i> Chaudoir
<i>O. shpeleyi</i> , new species	<i>O. championi</i> Bates
<i>O. pacifica</i> , new species	<i>O. donato</i> Ball and Shpeley
<i>O. aeneipennis</i> species group	<i>O. chrysura</i> Bates
<i>O. batesi</i> , new species	<i>O. kathleenae</i> , new species
<i>O. aeneipennis</i> Chaudoir	<i>O. exeuros</i> , new species
<i>O. cupricauda</i> Casey	<i>O. polytreta</i> , new species
<i>O. stenapteryx</i> , new species	<i>O. crabilli</i> , new species
<i>O. pallidipes</i> Chaudoir	<i>O. quadrispinosa</i> Bates
<i>O. rubida</i> Bates	<i>O. scintillans</i> , new species
<i>O. perissostigma</i> species group	<i>O. fulgens</i> Dejean
<i>O. perissostigma</i> , new species	<i>O. tricolor</i> Dejean
<i>O. pusilla</i> species group	<i>O. hoepfneri</i> Dejean
<i>O. pusilla</i> Chaudoir	<i>O. sallei</i> Chaudoir
<i>O. rawlini</i> , new species	

in the platynine group, with the implication that its truncatipennian (lebiomorph) features are convergent with that group, and do not comprise evidence of relationships.

What is *Onypterygia*? Although it is clearly a platynine, its position in the Platynini is not certain. This question remains as open now as when Whitehead (1973) surveyed the Mexican species of *Platynus*. The genus comprises the only beetles of the worldwide subtribe Platynina (sensu Habu, 1978) having pectinate tarsal claws, and its distribution is confined to the northern Neotropics. *Onypterygia* is distinguished from *Platynus* (Whitehead, 1973, and Liebherr, 1992) only by pectinate tarsal claws of adults. However, the pectinations are distinctive (long and curved mesoventrally), providing the basis to postulate that the genus is monophyletic.

Liebherr (1986:26) suggested that *Onypterygia* is derived from *Platynus*, and we do not disagree. However, we retain it as a genus because there is no formal reason to do otherwise. The approach is conservative: the genus has been considered valid since first proposed, and being still unbroken it requires no fixing.

Classification of Species

The 34 species of *Onypterygia* are arranged in seven species groups (Table 3). The Appendix (p. 408) provides an index to the names of the taxa, including junior synonyms.

Key to Adults of the Species of *Onypterygia* Dejean

- | | | |
|-------|--|---|
| 1 | Metathorax short, metepisternum with anterior and lateral margins about equal in length; metasternum between middle and hind coxae about half length of hind coxa | 2 |
| 1' | Metathorax longer (normally developed), metepisternum with lateral margin much longer than anterior margin; metasternum between middle and hind coxae equal or subequal in length to hind coxa | 7 |
| 2 (1) | Elytra bright metallic, striped alternately with metallic green and cupreous vittae; | |

- umbilical punctures foveate. Geographical range—Costa Rica *O. donato* Ball and Shpeley, p. 356
- 2' Elytra concolorous, slightly metallic or nonmetallic 3
- 3 (2') Pronotum with posterior pair of setigerous punctures distinctly anterad posterolateral angles (Fig. 30B). Color of body and elytra rufotestaceous. Interval 3 of elytron with only two setigerous punctures *O. shpeleyi*, n. sp., p. 319
- 3' Pronotum with posterior pair of setigerous punctures at or only slightly anterad posterolateral angles. Color of body and elytra rufotestaceous or darker 4
- 4 (3') Elytron with apex of suture (interval 1) angulate or denticulate 5
- 4' Sutural apex of elytron rounded, not angulate or denticulate 6
- 5 (4) Elytra with interneurs deep; interval 3 tri- or bisetose. Geographical range—Mexico: Sierra Madre del Sur, Guerrero *O. wappesi*, n. sp., p. 315
- 5' Elytra with interneurs evanescent; interval 3 bisetose. Geographical range—Mexico: Sierra Madre del Sur, Oaxaca *O. pacifica*, n. sp., p. 320
- 6 (4') Body and leg color darker, piceous, elytra dull blue-green. Geographical range—Mexico: Transvolcanic Sierra, State of México *O. amecameca*, n. sp., p. 317
- 6' Color of body, legs, and elytra paler, rufotestaceous. Geographical range—Mexico: Sierra Madre del Sur, Guerrero *O. atoyac*, n. sp., p. 318
- 7 (1') Elytron with interneurs more deeply (normal) engraved, interneur 1 on apical declivity not deeper than interval 2; preapical lateral callus absent; sutural apex not angulate or denticulate 8
- 7' Elytral interneur 1 near apex much deeper than interneur 2, or all interneurs shallowly engraved; preapical lateral callus distinct, indistinct, or absent; sutural apex angulate, denticulate, or rounded 19
- 8 (7) Elytron with apex sharply angulate or acuminate (cf. Fig. 10); color distinctly metallic or not 9
- 8' Elytron with apex rounded (cf. Fig. 7); color distinctly metallic 10
- 9 (8) Color of elytral disc bright metallic green, with cupreous overtones posteriorly. Pronotum (Fig. 49B) with lateral margins markedly sinuate posteriorly, and posterolateral angles more pointed. Internal sac of male genitalia without spinose sclerites. Geographical range—Mexico: Sierra Transvolcanica, Nayarit *O. rawlini*, n. sp., p. 341
- 9' Color of elytral disc either bronze or dull bronze-green. Pronotum (Fig. 49A) with lateral margins less sinuate posteriorly, posterolateral angles more rounded. Internal sac of male genitalia (Fig. 50B) with single (basal) spinose sclerite *O. pusilla* Bates, p. 339
- 10 (8') Hind femur with dorsoapical setae (one or more) 11
- 10' Hind femur without dorsoapical setae 12
- 11 (10) Elytra metallic, green in most specimens, with cupreous reflections apically. Pronotum with two pairs of lateral setigerous punctures *O. famini* Solier (in part), p. 309
- 11' Elytra metallic, blue in most specimens, without cupreous reflections apically. Pronotum with single pair (posterior) of lateral setigerous punctures *O. cyanea* Chaudoir, p. 312
- 12 (10') Head with pronounced frontal carina on each side. Pronotum slender, as long as or longer than wide (Fig. 19, 47) and posterolateral impressions coarsely punctate; prosternum with apex of intercoxal process truncate. Sternum VII of female with row of five or six pairs of setigerous punctures near posterior margin *O. perissostigma*, n. sp., p. 335
- 12' Head without distinct frontal carinae laterally. Pronotum broader, with posterolateral impressions impunctate or finely punctate; prosternum with intercoxal process rounded apically. Female sternum VII with two pairs of marginal setigerous punctures 13
- 13 (12') Pronotum in color entirely pale, or dark but with explanate lateral margins pale. Femora pale. Elytra metallic green or blue, without cupreous reflections apically. Geographical range—Mexico: Transvolcanic Sierra, Pacific drainages 14
- 13' Pronotum dark, including beaded or explanate lateral margins. Femora pale or dark. Elytra metallic green, with evident to pronounced cupreous reflections apically. Geographical range—Mexico to El Salvador 15
- 14 (13) Pronotum (Fig. 38) with lateral margins markedly sinuate posteriorly; posterolateral angles sharp. Geographical range—Mexico: Morelos and Puebla *O. pallidipes* Chaudoir, p. 330
- 14' Pronotum (Fig. 39) with lateral margins slightly sinuate posteriorly; posterolateral angles obtuse. Geographical range—Mexico: Michoacán and Colima *O. rubida* Bates, p. 332
- 15 (13') Pronotum (Fig. 21) with lateral margins not beaded, evenly curved, not sinuate poste-

- riorly; lateral grooves broad throughout their length. Geographical range—northeastern Mexico to El Salvador *O. famini* Solier (in part), p. 309
- 15' Pronotum (Fig. 34–37) with lateral margins distinctly beaded or not; distinctly sinuate posteriorly; lateral grooves narrow throughout or widened basally only. Geographical range—Mexico: Sierra Madre Oriental, Transvolcanic Sierra, or Sierra Madre del Sur 16
- 16 (15') Pronotum (Fig. 34) with lateral margins explanate, slightly sinuate posteriorly; postero-lateral angles obtuse; anterior lateral seta inserted ca. 1.5–3.0 diameter of setal puncture from margin. Geographical range—Mexico: Atlantic drainages of Sierra Madre Oriental, Transvolcanic Sierra, and Sierra Madre del Sur *O. batesi*, n. sp., p. 325
- 16' Pronotum (Fig. 35–37) with lateral margins explanate to narrow, distinctly to markedly sinuate posteriorly; posterolateral angles sharp; anterior lateral seta inserted ca. 1.0–1.5 diameter of setal puncture from lateral margin. Geographical range—Mexico: Pacific drainages of Transvolcanic Sierra and Sierra Madre del Sur 17
- 17 (16') Appendages paler, femora rufous to rufopiceous. Geographical range—Mexico: state of México, and Michoacán *O. stenapteryx*, n. sp., p. 329
- 17' Appendages darker, femora piceous to black. Geographical range—Mexico: Sierra Madre del Sur 18
- 18 (17') Pronotum (Fig. 35) narrower, values for LP/WP more than 0.95. Geographical range—Mexico: Oaxaca *O. aeneipennis* Chaudoir, p. 327
- 18' Pronotum (Fig. 36) broader, values for LP/WP less than 0.95. Geographical range—Mexico: Guerrero *O. cupricauda* Casey, p. 328
- 19 (7') Pronotum (Fig. 53) with lateral margins distinctly sinuate posteriorly; lateral setigerous punctures one or two pairs; posterolateral angles sharp. Sternum VII of male with single pair of posterior marginal setigerous punctures, females with two pairs 20
- 19' Pronotum (cf. Fig. 73) with lateral margins not distinctly sinuate; lateral setigerous punctures one or two pairs, or absent; posterolateral angles various, from nearly rectangular to distinctly rounded 23
- 20 (19) Pronotum with one pair (posterior) of lateral setigerous punctures 21
- 20' Pronotum with two pairs of lateral setigerous punctures 22
- 21 (20) Elytra green; apices obtusely angulate. Geographical range—Mexico: eastern Veracruz *O. pseudangustata*, n. sp., p. 347
- 21' Elytra coppery or coppery green; apices acuminate (Fig. 10). Geographical range—Mexico: eastern Oaxaca *O. striblingi*, n. sp., p. 348
- 22 (20') Elytron with apex acuminate (Fig. 10). Geographical range—Guatemala and Mexico: Chiapas *O. longispinis* Bates, p. 344
- 22' Elytron with apex obtusely angulate. Geographical range—Mexico: Veracruz to Panama *O. angustata* Chevrolat, p. 345
- 23 (19') Pronotum with two pairs of lateral setigerous punctures 24
- 23' Pronotum with one pair (posterior) of lateral setigerous punctures, anterior pair absent 27
- 24 (23) Elytra with alternating metallic green and cupreous vittae. Female with stylomere 2 of ovipositor slender, with few ensiform setae, and without lateral pad of setae (Fig. 12) 25
- 24' Elytra metallic green, without alternate metallic green and coppery vittae. Stylomere 2 (Fig. 16A) stout, with lateral pad of ensiform setae 26
- 25 (24) Elytron with apex broadly rounded, apex of interval 1 not angulate or denticulate. Sternum VII of female with more than two pairs of posterior marginal setae. Geographical range—Mexico: Veracruz *O. iris* Chaudoir, p. 353
- 25' Elytron with apex acuminate (Fig. 10), apex of interval 1 subangulate to denticulate. Geographical range—Panama and Costa Rica *O. championi* Bates, p. 354
- 26 (24') Elytron with apex obtusely angulate (Fig. 4B). Pronotum with lateral margins broad, not beaded; posterolateral angles obtuse, but evident. Elytron with interval 3 trisetose. Abdominal sternum VII of female with two pairs of posterior marginal setae. Geographical range—Mexico: Chiapas, to Costa Rica *O. chrysura* Bates, p. 356
- 26' Elytron with apex acuminate (Fig. 11A). Pronotum with lateral margins narrow, beaded; posterolateral angles broadly rounded. Elytron with interval 3 bisetose, anterior setigerous puncture absent. Sternum VII of female with more than two pairs of posterior marginal setae *O. kathleenae*, n. sp., p. 358
- 27 (23') Pronotum (Fig. 54A, B) with posterolateral angles angulate. Size smaller, TL less than 10.0 mm. Sternum VII of female with only two pairs of posterior marginal setae . . . 28

- 27' Pronotum (Fig. 67-74) with posterolateral angles rounded. Size larger, TL greater than 11.0 mm. Abdominal sternum VII of female with more than two pairs of marginal setae 29
- 28 (27) Elytra green; apices obtusely angulate. Geographical range—Mexico: eastern Veracruz *O. pseudangustata*, n. sp., p. 347
- 28' Elytra coppery or coppery green; apices acuminate (Fig. 10). Geographical range—Mexico: eastern Oaxaca *O. sriblingi*, n. sp., p. 348
- 29 (27') Elytron with disc plurifoveate; umbilicate setigerous punctures moderately to markedly foveate. Geographical range—Costa Rica to Panama 30
- 29' Elytron with disc not plurifoveate, setigerous punctures of interval 3 foveate or not; umbilicate setigerous punctures foveate or not. Geographical range—Mexico to Panama 31
- 30 (29) Elytra without alternate metallic green and coppery vittae; interneurs obsolete, each marked only by large punctures; interneur 1 toward apex not impressed. Geographical range—Costa Rica *O. crabilli*, n. sp., p. 362
- 30' Elytra with alternate metallic green and coppery vittae; interneurs each marked by row of fine, closely set punctures in addition to large foveae on intervals 3, 5, and 7 (Fig. 77); interneur 1 apically clearly impressed. Geographical range—Panama *O. polytreta*, n. sp., p. 361
- 31 (29') Pronotum (Fig. 67) with lateral margins posteriorly narrow, beaded. Elytron with apex acuminate (Fig. 11A), extended markedly. Geographical range—southern Mexico *O. exeuros*, n. sp., p. 359
- 31' Pronotum (Fig. 69) with lateral margins posteriorly wide, not beaded. Elytron with apex obtusely angulate to biacuminate 32
- 32 (31') Elytron with umbilicate series of setigerous punctures markedly foveate. 33
- 32' Elytron with umbilicate series not markedly foveate. 34
- 33 (32) Elytron with apex and sutural apex acuminate. Geographical range—Guatemala *O. quadrispinosa* Bates, p. 364
- 33' Elytron with apex rounded, apex of interval 1 (sutural apex) only angulate or denticulate, not acuminate. Geographical range—Costa Rica *O. scintillans*, n. sp., p. 365
- 34 (32') Pronotum without lateral setigerous punctures. Elytra metallic green or blue, with or without coppery reflections. Geographical range—northern Mexico to northern South America *O. fulgens* Dejean, p. 366
- 34' Pronotum with single pair (posterior) of lateral setigerous punctures. Elytra of various colors 35
- 35 (34') Elytra bicolored, basal half rufestaceous, apical half dark violaceous; apex of elytron sharply denticulate. Geographical range—northern Mexico to northern South America *O. tricolor* Dejean, p. 370
- 35' Elytra concolorous; apex of elytron sharply bidenticate or not 36
- 36 (35') Elytra shiny, each with conspicuous preapical callus, laterally. Pronotum with posterolateral impressions markedly punctate. Geographical range—Mexico: central Veracruz *O. sallei* Chaudoir, p. 377
- 36' Elytra less shiny, with preapical calli inconspicuous. Pronotum with posterolateral impressions not markedly punctate. Geographical range—central Mexico (excluding Veracruz) to Honduras *O. hoepfneri* Dejean, p. 375

The *famini* Species Group

Diagnostic Combination

With character states of *Onypterygia*, restricted as follows. Adults of this species group are small to moderate in size (TL 9–11 mm), with head dorsally and pronotum dark metallic green, elytra with disc concolorous metallic green or blue, with or without cupreous reflections laterally. Pronotal lateral setae one or two pairs, each elytron with three discal setae in or adjacent to interval 3, hind femur with or without dorsoapical setae, abdominal sterna IV–VI each with one pair of ambulatory setae, and sternum VII of males with one pair of posterior marginal setae, females with two pairs. Pronotum (Fig. 21, 22) with lateral margins curved evenly, or slightly sinuate posteriorly, not beaded, lateral grooves wide; posterior

pair of lateral setigerous punctures near posterolateral angles, slightly removed from margins. Elytral apices are broadly rounded (Fig. 7), sutural apices rounded, not denticulate (cf. Fig. 8), and dorsal surface without preapical lateral calli (cf. Fig. 11B:pc).

Description

With diagnostic combination of the *famini* species group and the following. Body of average appearance, size moderate, measurements and proportions as in Table 2.

Color.—Ventral surface of body and appendages (except apical antennomeres and elytra) black to piceous.

Microsculpture.—Head with mesh pattern clearly evident to indistinct, isodiametric, but on clypeus slightly transverse. Pronotum with mesh pattern transverse, microlines fine but evident throughout. Elytra with mesh pattern isodiametric, lines fine but evident throughout.

Luster.—Dorsal surface moderately shining.

Head.—Frons and vertex smooth, without supraorbital carina each side. Eyes of average convexity.

Prothorax.—Pronotum sparsely punctate posterolaterally; posterior pair of setigerous punctures near posterolateral angles. Anterior bead complete or incomplete; lateral beads absent medially and anteriorly; posterolateral impressions impunctate or sparsely punctate; posterolateral angles broadly rounded. Prosternum with intercoxal process rounded apically.

Pterothorax.—Mesepisternum generally punctate. Metathorax fully developed, metepisterna distinctly longer than wide.

Elytra.—Surface smooth. Elytron with humerus broadly rounded, developed normally; lateral margin slightly rounded; apex rounded; sutural apex rounded; discal and umbilical punctures not foveate. Interneurs 1 and 2 posteriorly on apical declivity about equally deeply impressed; interneurs 2–6 punctate for most of length.

Hind Wings.—Macropterous; wedge cell (Fig. 23:w) elongate, with short sides equal to one another.

Legs.—Tarsomeres 1–3 of middle and hind tarsi sulcate laterally. Fore tarsomere 4 with inner lobe longer than basal portion; hind tarsomere 4 with outer lobe shorter than basal portion. Tarsomeres 2–4 with climbing setae ventrally markedly dense (cf. Fig. 11F:cs). Tarsomere 5 with ventrolateral setae normally developed (cf. Fig. 11G:vs). Claws with pectinations more extensive (cf. Fig. 11H:p).

Male Genitalia.—Median lobe with apical portion short (Fig. 24A:ap), internal sac relatively short, with two or three patches of long setiform spines (Fig. 25C:s.sp), without basal or preapical lobes.

Ovipositor.—Stylomere 2 (Fig. 26) form 1, dorsolateral margin with about ten ensiform setae.

Habitat

Adults of this species group have been collected in tropical deciduous, tropical montane, oak, and oak–pine forests, from near sea level to 2300 m altitude.

Geographical Distribution

The range of this species group extends from northwestern Mexico southward to El Salvador (Fig. 27).

Chorological Affinities

Species of the *O. famini* species group are known to occur with those of the *aeneipennis*, *angustata*, *pusilla*, and *fulgens* species groups, and to overlap the ranges of the *wappesi* and *perissostigma* groups.

Included Species

Two species are included in this group: *O. famini* Solier and *O. cyanea* Chaudoir.

Onypterygia famini Solier

(Fig. 2, 6A–F, 7, 21, 23, 24, 26, 27)

Onypterygia famini Solier (1835:113). Type material: not found (expected to be in MNHP, and sought there unsuccessfully by Whitehead in 1968, and by Ball in 1972). Bates, 1882:131.

Onychopterygia famini; Gemminger and Harold, 1868:384. Chaudoir, 1878:276.

Onypterygia viridipennis Chevrolat, 1835:158. Lectotype (here designated): slightly teneral male in excellent condition, labelled “Chevrolat Carabidae. Fr. V. d. Poll. Pres. 1909 E. B. Poulton.” and

"TYPE COL: 148 2/2 *Onypterygia viridipennis* Chevr. HOPE DEPT. OXFORD" (OXUM). Chaudoir, 1878:276.

Onypterygia humilis Chevrolat, 1835:159. Lectotype (here designated): male labelled "*humilis* Chv. famini Sol. fulgidipennis Lap." and "Chevrolat Carabidae. Fr. V. d. Poll. Pres. 1909, E. B. Poulton." (OXUM). Chaudoir, 1878:276.

Onypterygia fulgidipennis Castelnau, 1840:42. Type material: not found (expected to be in MNHP, and sought there unsuccessfully by Whitehead in 1968, and by Ball in 1972). Chaudoir, 1878:276.

Type Material

We have not seen type material of *O. famini* or of *O. fulgidipennis*, but we accept the synonymy proposed by Chaudoir (1878:276). Specimens of *O. humilis* and *O. viridipennis* in Chevrolat material at the Hope Museum are fully typical of *O. famini*, and lectotypes were selected as indicated. The specimen of *O. humilis* was displaced in the collection, but according to Ernest Taylor (personal communication) it is the only specimen available as a possible type. A female specimen of *O. viridipennis* labelled "TYPE COL: 148 1/2. . ." in the Hope Museum is a composite of an *O. famini* hind body with the fore body of some other species.

Type Localities

The type area is Mexico for *O. famini*, *O. humilis*, and *O. fulgidipennis*. Here, we restrict the type locality to 10 km northwest of Jalapa. The type locality of *O. viridipennis* is Las Vigas, Veracruz, Mexico.

Diagnostic Combination

Adults of this species have the features of the *O. famini* species group, elytra metallic green with cupreous reflections laterally, and the pronotum with two pairs of marginal setae.

Description

With diagnostic combination of *O. famini* and the following.

Measurements and Proportions.—Size small to intermediate (TL 9.0–11.5 mm), WP/WH intermediate (1.31), LP/WP intermediate (0.90), WP/WPb low (1.20), LE/WE intermediate (1.64).

Color.—Apical antennomeres rufopiceous. Elytra bright green, laterally with cupreous reflections.

Microsculpture.—Elytra, as in Figure 2.

Chaetotaxy.—Pronotum, lateral setae two pairs.

Mouthparts.—Mandibles as in Figure 6A–F.

Prothorax.—Pronotum (Fig. 21). Anterior bead complete, or incomplete; posterolateral impressions sparsely punctate; angles broadly rounded; lateral margins sinuate.

Hind Wings.—Macropterous. Venation as in Figure 23.

Male Genitalia.—As in Figure 24A, B.

Ovipositor.—Stylomeres 1 and 2 as in Figure 26.

Variation

Pronotal form is quite varied, in some specimens much like that shown for *O. cyanea* (Fig. 22), except for having both pairs of marginal setae. Pronotal sides tend to be more markedly sinuate and the posterolateral angles more prominent in specimens from Hidalgo, San Luis Potosi, and Veracruz than in specimens from Chiapas, but extremes are present in both areas. One specimen from near Chiapa de Corzo is notably small, relatively dull (metallic luster slight), and has convex elytral intervals and relatively coarse microsculpture. The elytra of a specimen from Los Amates appear blue from above but are clearly green and faintly cupreous from behind.

Habitat

Specimens of *O. famini* have been taken in moderately dry to moderately wet forests, chiefly oak, at middle altitudes (732–2286 m) in Mexico. Specimens have been taken in bromeliads (December, January, February, April, and May), others at UV lights (May and June), and some in moss on rocks (November). These records suggest active flight during the summer wet season and adult quiescence in the winter dry season.

In Guatemala, several specimens of this species were collected at night, at UV light traps, in tropical montane forest. In spite of intensive efforts to find them, no specimens were collected in the vicinity of the light traps during daylight hours, and so perhaps the nocturnally active individuals had flown into the area from elsewhere.

Geographical Distribution

The range of *O. famini* extends from San Luis Potosi in northeastern Mexico and the Sierra Madre del Sur in Oaxaca south at least to El Salvador, and perhaps Costa Rica (Fig. 27). We have not verified Middle American records listed by Bates (1882:131), but we found specimens from all Mexican localities except Las Vigas, Veracruz, in BMNH and MNHP. The record from Puebla may refer to a locality other than the city of that name.

Chorological Affinities

The range of *O. famini* is allopatric in relation to the range of its close relative, *O. cyanea* (Fig. 27).

Phylogenetic Relationships

This species is postulated to be the adelphotaxon of *O. cyanea* Chaudoir. Although the two species seem to be closely related on the basis of many shared features, and although they are parapatric or marginally sympatric, we have not seen evidence of intergradation.

Material Examined

About 130 specimens of *O. famini* were seen, from the following localities. **MEXICO. Chiapas:** 11.5 km S Amatenango del Valle. Jct. Hwy. 190 & 195, nr. Chiapa de Corzo. 1 male, 2 km S Chicoasén, on rd. to Mirador, VI.18.1989, H. F. Howden (UASM); 1 female, El Chorreadero, 8 km E Chiapa de Corzo, VI.6.1989, H. F. Howden (UASM); 1 male, El Aguacoero Parque, VI.22.1990, J. Huether (JEW); 3 males, 3 females, 4.8 & 12.4 km S Frontera Comalapa, 743 m, U-V light, VI.15–17.1966, Ball & Whitehead (UASM); 1 male, 47 km N. Huixtla, 1311 m, bromeliads, II.26.1966, Ball & Whitehead (UASM); Los Amates (UASM); 1 female, 1 km S Ocosingo, X.18.1988, H. & A. Howden (RH); 1 female, 5 km E Ocozocoautla, 820 m, VI.4.1990, H. & A. Howden (UASM); 1 male, 1 female, Parque Nacional Sumidero, 1000 m, V.25.1990, H. & A. Howden (UASM); 1 male, 3 females, 5 km S Pueblo Nuevo, 1646 m, in bromeliads, IV.27.1966 (UASM); 1 female, Rancho Nuevo, 14 km SE San Cristóbal de las Casas, VIII.30.1965, D. E. Breedlove (CASC); Ruinas Chincultic, 1500 m—3 males, VI.3.1990, H. & A. Howden (CMNC); 2 females, VI.12.1989, H. F. Howden (UASM); 1 male, 1 female, VI.12.1990 (UASM); 1 male, 3 females, Clark & Cave (AU); 1 male, X.18.1988, R. H. Turnbow (RH); San Cristóbal de las Casas (UASM); 27.4 km SE Teopisca (UASM). **Hidalgo:** 1 female, Atexca, V.26.1979, M. Zunino (ACCS); NE Jacala—1 female, 38 km, 1372 m, V.27.1974 (UASM); 2 males, 1 female, V.27.1974, O'Brien, O'Brien & Marshall (UASM); 3 males, 2 females, 46.7 km, V.27.1974, O'Brien & Marshall (UASM). **Oaxaca:** 30 km S Sola de Vega (UASM). **Puebla:** Puebla. 1 male, Xicoteppec de Juárez, 1200 m, at mercury light (CASC). **San Luis Potosí:** 1 female, 30 km E Landa de Matamoros, 1524 m, XI.18–19, 1965, Ball & Whitehead (UASM); 1 male, Xilitla, VI.17.1963, D. R. Whitehead (UASM). **Veracruz:** Cerro de Palmas. Jalapa. 5 and 10 km NW Jalapa; 35 km E Jilotepec. Las Vigas (Bates, 1882); Orizaba; 1 female, Orizaba, Mann & Skewers (MCZ); 1 male, Río Juwapa, XI.6.1975, D. Figueroa (UNAM). **COSTA RICA.** Costa Rica (Bates, 1882). **EL SALVADOR. La Libertad:** Boquerón. **GUATEMALA. Alta Verapaz:** Senahú (Bates, 1882). **Baja Verapaz:** 1 male, 9.6 km W Chilascó, 1560 m,

humid oak-pine forest, U-V light, 91-21, V.25.1991 (UASM); Purulhá (Bates, 1882); 8 km S Purulhá, 1660 m, tropical montane forest, U-V light, Ball, Ball & Shpeley (UASM)—1 male, 1 female, V.19.1991; 2 males, 1 female, V.20.1991; 1 female, VI.1.1991. **Huehuetenango**: 55 km NW Huehuetenango, Río Selegua. **Sacatepequez**: Capetillo (Bates, 1882).

Onypterygia cyanea Chaudoir

(Fig. 22, 25A-D, 27)

Onychopterygia cyanea Chaudoir, 1878:277. Lectotype (here selected): male, labelled "Ex Musaeo Chaudoir" (Chaudoir-Oberthür box 293/2/5, MNHP).

Onypterygia cyanea; Bates, 1882:132.

Onypterygia valdestriata Bates, 1884:286. Type specimen: male, labelled "TYPE H. T." [circular, ringed with red], B.C.A. COL. I.1. *Onypterygia valdestriata*, Bates", "Pinos Altos, Chihuahua, Mexico. Buchan-Hepburn" (Drawer 361/4/5, BMNH). New synonymy.

Type Material

Onypterygia cyanea was described explicitly from Oaxaca, based on four specimens of Sallé material. We found no specimens so labelled in Chaudoir material (MNHP), but did find one male and two females without locality data; the male is selected here as lectotype.

Type Localities

For *O. cyanea*, the type locality is Oaxaca, Mexico. For *O. valdestriata*, it is Pinos Altos, Chihuahua. Bates cited the type locality of *O. valdestriata* as "Chihuahua" only, but labelling on the holotype is more specific.

Diagnostic Combination

With character states of the *O. famini* species group, restricted as follows. With noncupreous, blue (few specimens green or purple) elytra and only one (postero-lateral) pair of marginal setae on pronotum; apical antennomeres rufous (slightly paler than those of *O. famini*).

Description

With diagnostic combination of *O. cyanea* and the following.

Measurements and Proportions.—TL intermediate (9.5–10.5 mm); (proportions for male from 8.7 km E Cuernavaca, Morelos), WP/WH intermediate (1.38), LP/WP intermediate (0.90), WP/WPb low (1.19), LE/WE intermediate (1.65). Same of male from Sierra Charuco, Río Mayo, Sonora: WP/WH 1.34, LP/WP 0.92, WP/WPb 1.17, LE/WE 1.53.

Prothorax.—Pronotum (Fig. 22): posterolateral impressions impunctate, or sparsely punctate.

Male Genitalia.—As in Figure 25A–D.

Variation

Elytra are notably greenish in a specimen from Atzimba, notably purplish in one from Pinos Altos. Pronotal form varies much as in *O. famini*; most specimens from Morelos have markedly sinuate lateral margins and distinct posterolateral angles, and so resemble more closely specimens of *O. famini* from Veracruz than from Chiapas. Specimens from Sonora and Chihuahua differ from all others by much more distinct punctation on elytral interneurs, sides of metasterna, mesepisterna, and proepisterna; they may differ also by smaller patches of spines on the internal sac and by some body proportions.

Habitat

This species lives in more arid regions than does *O. famini*. Most records are from early June to early August, but one is from September (Cuernavaca). There are no dry season records, nor records from bromeliads. The longest series (eight specimens) was collected at UV light, in tropical deciduous forest, 8.7 km east of Cuernavaca, Morelos, June 29–30, 1966.

Geographical Distribution

The range of this species extends from western Mexico (Sonora and Chihuahua) south to Oaxaca (Fig. 27).

Chorological Affinities and Phylogenetic Relationships

See these topics for *O. famini*, above.

Material Examined

Approximately 120 specimens of *O. cyanea* were seen, from the following localities. Specimens from all localities listed by Bates (1882:132) are in BMNH or MNHP.

MEXICO. Chihuahua: 6 males, 6 females, 6.4 km N. Las Chinacas, 1271 m, U-V light, VII.9–10.1989, S. McCleve (UASM); Pinos Altos (Bates, 1882); 1 female, 9.7 km S Yécora (Sonora), 1752 m, U-V light, VII.2–3.1990, S. McCleve (UASM). **Colima:** 14.5 km N Comala; 2 males, 2 females, El Terrero, X.4.1992, R. H. Turnbow (RHTC); 3 females, W. rd. to El Terrero, 914.4–1524 m, X.3–5.1992, J. E. Wappes (JEW); 1 male, 3 females, 38.4 km W Villa Alvarez, X.5.1992, R. H. Turnbow (RHTC). **Durango:** 1 male, 3.2 km N. Pueblo Nuevo, R. H. Scheibner (MSUC). **Guerrero:** 1 female, Acahuizotla, VI.22.1982, M. Garcia (CASC); 4 km NE Cacahuamilpa (TAMU). Chilpancingo (USNM); 29 km S Chilpancingo; 15.4 km SW jct. Hwy 195 & rd. to Filo de Caballo (UASM); Taxco (CASC); Rte. 134, 67.1 km NE jct. w/Hwy 200 (UASM); 1 male, 8 km S Mazatlán, Hwy. 95, 830 m, VI.29.1992, C. L. Bellamy (CMNH). **Jalisco:** Ajijic (UASM); 1 male, 20 km N. Autlán, IX.28.1991, J. E. Wappes (JEW); 32 km SW Autlán (CDAE). 11.7 km S Cocula (UASM); 1 female, Microondas San Francisco (Autlán), X.6.1992, R. H. Turnbow (RHTC); 1 female, 10 km W Chapala, VI.30.1963 (CISC); 1 male, Guadalajara (CMNH); 2 males, 1 female, 33.8 km S Puerto Vallarta, Hwy. 200, 725 m, U-V light, S. McCleve, P. Jump (UASM); 1 female, Puerto Vallarta, VI.19.1961, P. R. Grant (CNCI). **México:** 5 & 7 km NE Ixtapan (TAMU); Temascaltepec (CASC). **Michoacán:** 1 male, 19 km S Tzitzio on Huetamo rd., 19°20'N., 100°50'W., VII.10.1947, T. H. Hubbell (UMMZ). **Morelos:** Alpuyeca (USNM); Cuernavaca (USNM); 1 male, Cuautla, VI.20.1971, H. Brailovsky (CUIC); 1 male, 1 female, 19 km E Cuernavaca, Cañon de Lobos, 1120–1375 m, VII.3.1992, C. L. Bellamy (CMNH). **Nayarit:** 1 female, 21 km W Chapalilla, X.9.1992, R. H. Turnbow (RHTC); 9.7 km N. Compostela. 1 female, El Pichón, VI.29.1963, J. Doyen (CISC); La Mesa de Nayar (CASC); Tepic (CDAE); 2 males, 7 females, 23 km S Tepic, 1067 m, VII.17.1977, J. E. Rawlins (CMNH); 37 km SE Tepic; 1 male, 2 females, Volcán Ceboruco, 4–11 km W Jala, X.8–9.1992, R. H. Turnbow (RHTC). **Oaxaca:** Ixtapa; 1 male, Km 30, Carretero Miahuatlán–Puerto Angel, 2200 m, X.21.1982, H. Brailovsky (CASC); 2 males, 1 female, Mun. Juquila, San Juan Lachao, IV.14.1965, G. Halfiter (CNCI). **Sinaloa:** 1 female, 6–7 km N. La Capilla del Taxte, X.5.1990, R. H. Turnbow (RHTC); 2 males, 7 km NE La Capilla del Taxte, VI.27.1977, J. E. Rawlins (CMNH); 1 male, 13 km W El Palmito, VII.1964, H. F. Howden (CNCI). **Sonora:** 2 males, 1 female, 5.1 km NW Huiboche, 1577 m, U-V light, VII.11–13.1989, S. McCleve (UASM); Sierra Charuco, Río Mayo; 1 male, 6.1 km S Santa Rosa, 1000 m, U-V light, Sinaloan thorn scrub, VII.09.1993, S. McCleve, G. E. & K. E. Ball (UASM); 1 male, 23.2 km NW Yécora, 1680 m, U-V light VII.08.1993, S. McCleve, G. E. & K. E. Ball (UASM); 1 male, 6.4 km NE Yécora, 1547 m, VI.30–VII.1.1990, S. McCleve (UASM).

The *wappesi* Species Group

Diagnostic Combination

With character states of *Onypterygia*, restricted as follows. Adults of this species group are small in size (TL ca. 5–8 mm), head dorsally and pronotum rufous to black, elytra dull metallic green or blue, without cupreous reflections, or piceous or rufous. Pronotal lateral setae one or two pairs, each elytron with two or three discal setae in or adjacent to interval 3, hind femur without dorsoapical setae, abdominal sterna IV–VI each with one pair of ambulatory setae, and abdominal sternum VII of males with one pair of posterior marginal setae, females with two pairs. Pronotum (Fig. 28–30B) with lateral grooves narrow, lateral margins posteriorly slightly sinuate or not, laterally and anteriorly beaded or not, and posterior pair of lateral setigerous punctures slightly or markedly anterad posterolateral angles, removed from lateral margins not on beads. Metathorax short, metepisternum quadrate, with anterior and lateral margins about equal to one

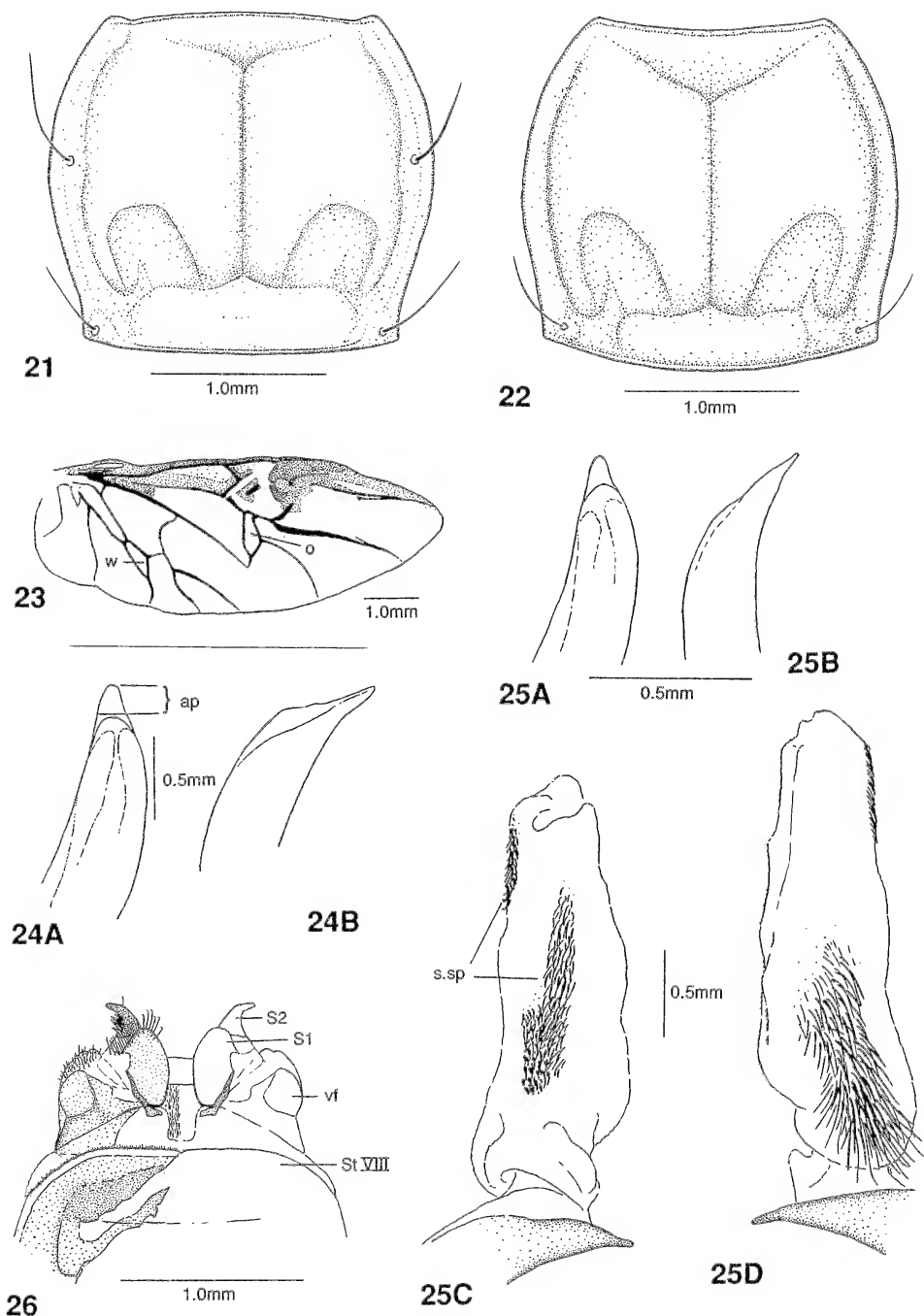


Fig. 21–26.—Line drawings of adult structural features of species of the *O. famini* group. Fig. 21, 22, pronotum, dorsal aspect: 21, *O. famini* Solier; 22, *O. cyanea* Chaudoir. Fig. 23, left hind wing of *O. famini* Solier. Fig. 24, 25, male genitalia: 24, *O. famini* Solier: A and B, median lobe, apical portion, dorsal and left lateral aspects, respectively; 25, *O. cyanea* Chaudoir: A, B, median lobe, dorsal and lateral aspects, respectively; C, D, internal sac, left and right lateral aspects, respectively, showing

another. Elytral apex rounded, sutural apex denticulate or rounded, interneurs about equally distinct, and preapical lateral calli absent.

Description

With diagnostic combination of *famini* group, and the following. Body rather small on average, measurements and proportions as in Table 2.

Color.—Body and appendages (except elytra) piceous to rufous only; elytra dull metallic green or blue, without cupreous reflections, to rufous (same color as body); other appendages of same color as body.

Microsculpture.—Head dorsally with microlines fine, nearly effaced, mesh pattern isodiametric. Pronotum with microlines very fine, nearly effaced, mesh pattern transverse. Elytra with microlines distinct, mesh pattern isodiametric or markedly transverse.

Luster.—Dorsal surface dull to moderately bright, elytra slightly iridescent or not.

Head.—Frons and vertex smooth, without supraorbital carina each side. Genae smooth, not rugose. Eyes moderately prominent, convexity average.

Prothorax.—Pronotum (Fig. 28–30B), surface sparsely punctate posterolaterally; lateral margins beaded or not, slightly sinuate posteriorly or not; posterolateral angles various. Prosternum with intercoxal process rounded apically.

Elytra.—Humeri sloped, not rounded. Discal and umbilical setigerous punctures not foveate. Interneurs 1 and 2 posteriorly on apical declivity about equally deeply impressed, or interneurs virtually absent, surface nearly smooth.

Hind Wings.—Brachypterous, short stubs.

Legs.—Tarsomeres 2–4 with climbing setae ventrally markedly dense (cf. Fig. 11F:cs). Tarsomere 5 with ventrolateral setae normally developed (cf. 11G:vs). Claws with pectinations more extensive (cf. Fig. 11H:p).

Male Genitalia.—Median lobe with apical portion short, apex narrowly rounded (Fig. 31A, B). Internal sac variously armored: with single left median spinose sclerite (Fig. 32B, C), with basal and median ventral spinose sclerites (Fig. 31C), or without spinose sclerites (Fig. 32A).

Ovipositor.—Stylomere 2 form 1, as in Figure 12A, with about eight ensiform setae on or near dorsolateral margin.

Habitat

The species of the *wappesi* species group occupy tropical montane, riparian–alder, and dry pine–oak forests, from about 1700 to 2200 m altitude.

Geographical Distribution

This group is known only from Mexico, on the lower western slopes of the Sierra Madre del Sur, and from the Transvolcanic Sierra (Fig. 33).

Chorological Affinities

See “Chorological Affinities” for *famini* species group, above.

Included Species

Five species are included, all undescribed: *O. wappesi*, *O. amecameca*, *O. atoyac*, *O. shpeleyi*, and *O. pacifica*.

Onypterygia wappesi, new species (Fig. 8, 12, 28, 31A–C, 33)

Type Material

Eleven specimens. Holotype male, labelled: “MEX., Guerrero/Hwy 134, 67 km NE/jct 200, VII.14.85/J. E. Wappes” (USNM). Allotype female, labelled same as

←

spine fields. Fig. 26, sternum VIII and ovipositor sclerites of *O. famini* Solier. Legend: ap—median lobe, apical portion; o—oblongum cell; S1, S2—stylomeres 1 and 2, respectively; S.sp.—setiform spine; St VIII—sternum VIII; Vf—valvifer; w—wedge cell.

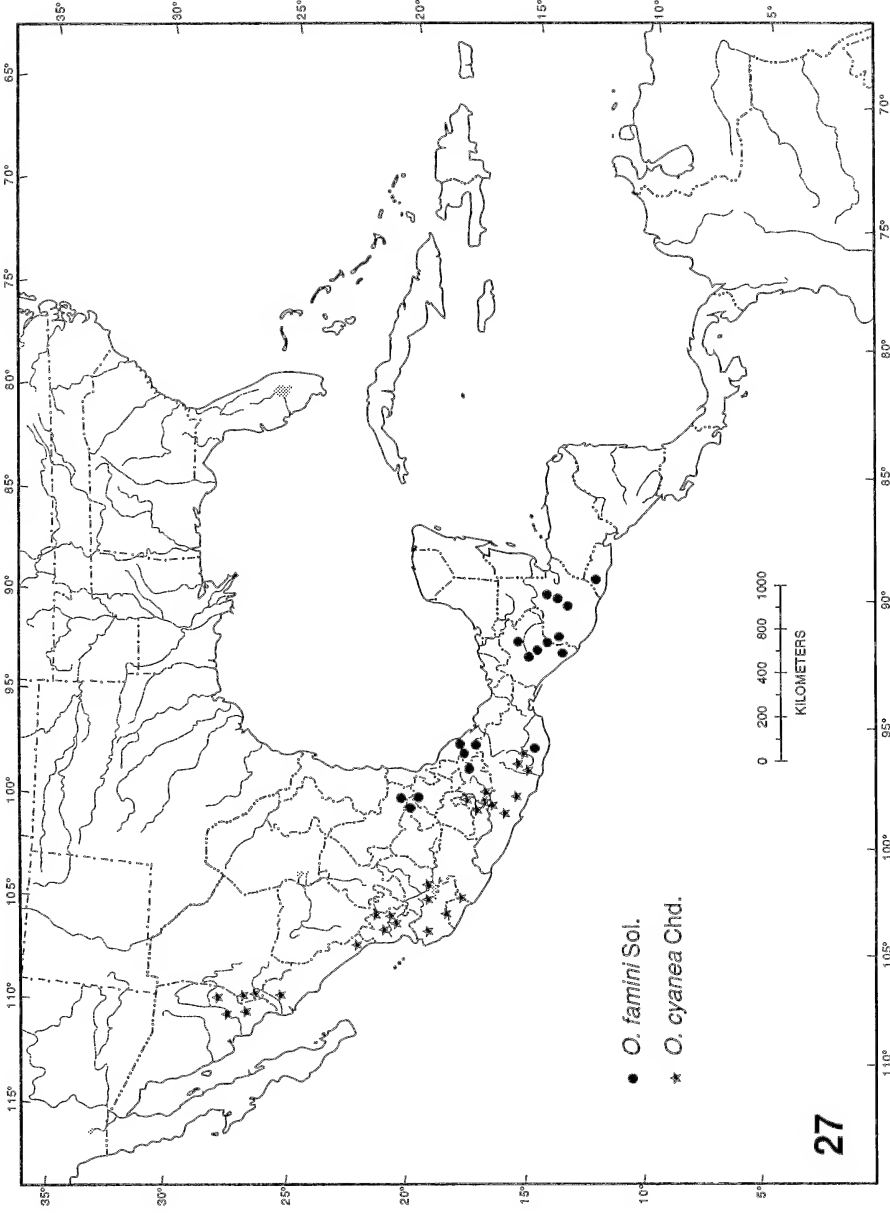


Fig. 27.—Map of southern North America, Middle, and northern South America, showing approximate positions of collecting records for species of the *O. famini* group.

holotype (USNM). Paratypes, nine females, one labelled same as holotype (JEWG), eight labelled: "MEXICO Guerrero/hwy. 134 66.4 km NE jct./Hwy 200, 15 July 1985/R. Turnbow" (BMNH, CUIG, MNHP, RHTC, UASM).

Specific Epithet

Based on the surname of our friend, James E. Wappes, who, during his many trips to Middle America to collect cerambycids, has collected numerous carabids from interesting localities, and has made them available to us for study.

Diagnostic Combination

With character states of *O. wappesi* species group, and combination of rufopiceous color, small posterolateral pronotal impressions, elytral interneurs of average depth, angulate sutural apices, and trisetose interval 3.

Description

With diagnostic combination of *O. wappesi* and the following.

Measurements and Proportions of Holotype.—TL small (8.8 mm), WP/WH low (1.56), LP/WP low (0.86), WP/WPb high (1.40), LE/WE low (1.48).

Color.—Head piceous-black. Antennae with basal and apical antennomeres rufopiceous. Palpi piceous. Pronotum piceous-black. Elytra with discal pattern concolorous, dull green. Femora rufopiceous; tibiae and tarsi rufopiceous.

Microsculpture.—Mesh pattern of elytra, isodiametric.

Chaetotaxy.—Pronotum, lateral setae two pairs; elytron, discal setae three.

Prothorax.—Pronotum (Fig. 28). Anterior bead complete. Lateral margins not sinuate, beaded narrowly, posterolateral pair of setigerous punctures slightly in advance of posterolateral angles.

Pterothorax.—Mesepisternum generally punctate.

Elytra.—Elytron (Fig. 8) with lateral margin broadly rounded; sutural apex rounded. Interneurs 2–6 continuous, moderately deep, punctate for part of length.

Legs.—Tarsomeres 1–3 of midtarsi and hind tarsi sulcate. Fore tarsomere 4, inner lobe as long as basal portion; hind tarsomere 4, outer lobe shorter than basal portion.

Male Genitalia.—(Fig. 31A–C) Median lobe, apical portion short; apex narrowly rounded. Internal sac relatively short; basal lobes absent; preapical lobes absent; armature one spinose sclerite.

Ovipositor.—Stylomeres 1 and 2 as in Figure 12.

Geographical Distribution

This species is known from the localities for the type series only (Fig. 33).

Chorological Affinities

Localities for this species, *O. shpeleyi*, and *O. atoyac* are in close proximity. Probably they are sympatric. Additionally, *O. cupricauda* (*aeneipennis* species group) probably is sympatric with *O. wappesi*, and the wide-ranging species of the *fulgens* species group probably occur in the same area, as well.

Material Examined

We saw the type series only; see above for details.

Onypterygia amecameca, new species

(Fig. 33)

Type Material

Holotype female, labelled: "Amecameca/ Mex./VII.8.1897"; "Koebele Collection" [dull orange paper]; "PN drawn/D. Hollingdale/1990" (CASC).

Type Locality

Amecameca, state of México, Mexico.

Specific Epithet

A noun in apposition, based on the name of the type locality.

Diagnostic Combination

With character states of the *O. wappesi* species group, restricted as follows. Body and legs piceous, elytra rather dull metallic blue-green, pronotum with posterolateral angles obtusely angulate, posterolateral impressions broad, coextensive laterally with lateral grooves, elytra with interneurs shallow but sharp basally, less distinct on apical declivity, scutellar apices rounded, and interval 3 bisetose.

Description

With diagnostic combination of *O. amecameca*, and the following.

Measurements and Proportions of Holotype.—TL small (5.20 mm), WP/WH low (1.41), LP/WP low (0.83), WP/WPb low (1.20), LE/WE low (1.42).

Color.—Head piceous-black. Antennae with basal and apical antennomeres rufotestaceous, or testaceous. Palpi piceous. Pronotum piceous-black. Elytra with discal pattern concolorous; blue-dull. Femora rufopiceous; tibiae and tarsi rufopiceous.

Microsculpture, Mesh Pattern.—Elytra, isodiametric.

Chaetotaxy.—Pronotum, lateral setae two pairs; elytron, discal setae two.

Prothorax.—Pronotum. Anterior bead complete. Lateral beads absent. Lateral margins sinuate, beaded posteriorly. Posterolateral pair of setigerous punctures at posterolateral angles.

Pterothorax.—Mesepisternum partially punctate.

Elytra.—Elytron, lateral margin broadly rounded. Apex rounded; sutural apex rounded. Interneurs 2–6 continuous, shallow, impunctate.

Legs.—Tarsomeres 1–3 of mid- and hind tarsi sulcate. Fore tarsomere 4, inner lobe shorter than basal portion; hind tarsomere 4, outer lobe shorter than basal portion.

Geographical Distribution

This species is known from the type locality only, which is located in a high-altitude internal drainage basin (Fig. 33).

Chorological Affinities

Onypterygia amecameca is widely isolated from the other members of the *wappesi* species group. *Onypterygia fulgens* (*fulgens* species group) might be sympatric with *O. amecameca*.

Material Examined

We have seen the holotype of *O. amecameca* only; see above for details.

Onypterygia atoyac, new species (Fig. 30A, 32B, 33)

Type Material

Holotype female, labelled: "MEX. Guer. 73.8km/ne Atoyac de Alvarez/cloud for.: stream,/arroyo; litter; 2340 m/August 12, 1983 83-75"; "MEXICO EXPED. 1983/H. E. Frania & R. J. Jaaqumagi/Collectors"; "PN DRAWN/D. Hollingdale/1990" (USNM).

Type Locality

73.8 km northeast of Atoyac de Alvarez, Guerrero, Mexico.

Specific Epithet

A noun in apposition, based on the name of the mountain range within which the type locality is located.

Diagnostic Combination

Character states of the *O. wappesi* species group, and integument generally rufous (specimen may be teneral), shining but not metallic, pronotum with posterolateral impressions narrow, lateral margins evenly constricted posteriorly, not sinuate, posterolateral angles obtuse, angulate, elytral interneurs shallow but distinct, punctate, elytral apices rounded, and interval 3 bisetose.

Description

With diagnostic combination of *O. atoyac* and the following.

Measurements and Proportions of Holotype.—TL small (5.2 mm), WP/WH low (1.38), LP/WP low (0.78), WP/WPb intermediate (1.29), LE/WE low (1.47).

Color.—Head rufopiceous. Antennae with basal and apical antennomeres testaceous. Palpi rufous. Pronotum rufopiceous. Elytra with discal pattern concolorous, bronze; epipleura testaceous, same as ventral surface. Femora rufotestaceous; tibiae and tarsi rufotestaceous.

Microsculpture, Mesh Pattern.—Elytra, isodiametric.

Chaetotaxy.—Pronotum, lateral setae two pairs. Elytron, discal setae two.

Prothorax.—Pronotum (Fig. 30A). Anterior bead complete. Lateral margins sinuate, not beaded. Posterolateral pair of setigerous punctures at posterolateral angles.

Pterothorax.—Mesepisternum partially punctate.

Elytra.—Elytron, lateral margin broadly rounded. Apex rounded; sutural apex rounded. Interneurs 2–6 continuous, shallow; impunctate.

Legs.—Tarsomeres 1–3 of mid- and hind tarsi sulcate. Fore tarsomere 4, inner lobe as long as basal portion; hind tarsomere 4, outer lobe shorter than basal portion.

Male Genitalia.—(Fig. 32B) Median lobe, apical portion short; apex narrowly rounded. Internal sac relatively short; armature, one spinose sclerite on left side; microtrichial fields extensive, microtrichia short, pointed sharply.

Geographical Distribution

Known from the type locality only, in the western part of the Sierra Madre del Sur (Fig. 33).

Chorological Affinities

The known localities for this species, *O. wappesi* and *O. shpeleyi*, n. sp., are in the Sierra Madre del Sur, and the three may be sympatric.

Material Examined

We have seen the type series of *O. atoyac* only; see above for details.

Onypterygia shpeleyi, new species (Fig. 30B, 32C, 33)

Type Material

Holotype male, labelled: "MEXICO Gro. 71 km/ne Atoyac de Alvarez/cloud for., 1700 m/beating vegetation/27.07.1992"; "D. Shpeley, H. E. Frania & J. S. Ashe collectors (USNM). Allotype female (USNM) and paratypes five males, three females, labelled same as holotype. Paratypes are distributed as follows: male, female (BMNH); male, female (MNHP); male (CMNC); two males, female (UASM).

Type Locality

71 km northeast of Atoyac de Alvarez, Guerrero, Mexico.

Specific Epithet

The Latinized genitive form of the surname of the collector of the type series, this name honors Danny Shpeley, Department of Biological Sciences, University of Alberta, in recognition of his substantial contributions in the collection, preparation, analysis, and taxonomic treatment of the Carabidae of the Neotropical region.

Diagnostic Combination

With character states of the *O. wappesi* species group, restricted as follows. In addition to character states noted in the key, adults of this species are recognized by a combination of elongate pronotum, sloped elytral humeri, and transverse microsculpture mesh of the elytra. Males are distinguished by form of apex of the median lobe (acuminate in dorsal aspect) and by the armature of the internal sac (single spinose sclerite on the left side, approximately medial in position).

Description

With diagnostic combination of *O. shpeleyi* and the following.

Measurements and Proportions of Holotype.—TL small (7.3 mm), WP/WH low (1.50), LP/WP low (1.00), WP/WPb intermediate (1.50), LE/WE low (1.60).

Color.—Head rufous. Antennae with basal articles rufotestaceous; apical articles rufopiceous. Palpi rufous. Pronotum rufous. Elytra with discal pattern concolorous, rufous. Femora, tibiae, and tarsi rufous.

Microsculpture, Mesh Pattern.—Elytra, transverse.

Chaetotaxy.—Pronotum, lateral setae two pairs; elytron, discal setae two.

Prothorax.—Pronotum (Fig. 30B). Anterior bead incomplete. Lateral margins not sinuate, beaded posteriorly only. Posterolateral pair of setigerous punctures markedly anterad posterolateral angles.

Pterothorax.—Mesepisternum impunctate.

Elytra.—Elytron, lateral margin narrowly rounded. Apex rounded; sutural apex rounded. Interneurs 2–6 continuous, moderately deep; punctate for most of length.

Legs.—Tarsomeres 1–3 of mid- and hind tarsi sulcate. Fore tarsomere 4, inner lobe longer than basal portion; hind tarsomere 4, outer lobe shorter than basal portion.

Male Genitalia.—(Fig. 32C) Median lobe, apical portion short; apex acute. Internal sac relatively short; armature, one spinose sclerite.

Habitat

Specimens were collected in cloud forest, from low vegetation (ca. 1 m high) with vines, the latter forming a tangled mass, with dry leaves suspended on them. A beating sheet was used, about 0.8 m above the ground.

Geographical Distribution

Known from the type locality only, in the western part of the Sierra Madre del Sur (Fig. 33).

Chorological Affinities

The locality of this species is close to those for *O. wappesi* and *O. atoyac*, and the three species probably are sympatric.

Material Examined

We have seen the type series of *O. shpeleyi* only; see above for details.

Onypterygia pacifica, new species

(Fig. 17, 32A, 33)

Type Material

Four specimens. Holotype male, labelled: "MEXICO: Oaxaca/2 miles north/San Jose Pacifico/July 16, 1974/Clark, Murray/Ashe, Schaffner" (TAMU). Allotype female, labelled same as holotype, except date: "July 20, 1974" (TAMU). Paratype female, labelled: "MEXICO: Oaxaca, 4.6 km/S. Suchixtepec, 2150 m/23.VII.1992 92.023, R. S./Anderson, wet ripar alder/for., leaf litter berlese" (USNM). Paratype male, labelled: "MEXICO: Oaxaca, 10.0 km/S. Suchixtepec, 2000 m/24.VII.1992 92.025, R. S./Anderson, roadside, beating" (CMNC).

Type Locality

The type locality is 3.2 km north of San José Pacífico, Oaxaca, Mexico.

Specific Epithet

An adjective, based on part of the Latinized name of the type locality.

Diagnostic Combination

With character states of the *O. wappesi* species group, restricted as follows. Color rufocastaneous; posterolateral impressions of pronotum small; elytra with striae evanescent, sutural apices angulate, and interval 3 bisetose.

Description

With diagnostic character states of *O. pacifica* and the following.

Habitus.—As in Figure 17.

Measurements and Proportions of Holotype.—TL small (7.1 mm), WP/WH low (1.44), LP/WP low (0.88), WP/WPb intermediate (1.38), LE/WE low (1.55).

Color.—Head rufous. Antennae with basal and apical antennomeres rufotestaceous. Palpi piceous. Pronotum rufous. Elytra with discal pattern concolorous, bronze; epipleura testaceous, distinctly paler than ventral surface. Femora rufopiceous; tibiae and tarsi rufopiceous.

Microsculpture, Mesh Pattern.—Elytra, isodiametric.

Chaetotaxy.—Pronotum. Lateral setae two pairs. Elytron, discal setae two.

Prothorax.—Pronotum. Anterior bead complete. Lateral margins not sinuate, beaded posteriorly only. Posterolateral pair of setigerous punctures slightly in advance of posterolateral angles.

Pterothorax.—Mesepisternum generally punctate.

Elytra.—Elytron, lateral margin slightly rounded. Apex rounded; sutural apex rounded. Interneurs 2–6 evanescent and punctate for part of length.

Legs.—Tarsomeres 1–3 of middle and hind tarsi sulcate. Fore tarsomere 4, inner lobe as long as basal portion; hind tarsomere 4, outer lobe shorter than basal portion.

Male Genitalia.—(Fig. 32A) Median lobe, apical portion short; apex narrowly rounded. Internal sac relatively short; armature, microtrichial patches.

Habitat

Adults have been collected in leaf litter in wet riparian montane forest, and in roadside vegetation, near such forest.

Geographical Distribution

This species is known only from the Oaxacan Sierra Madre del Sur (Fig. 33).

Chorological Affinities

The range of *O. pacifica* does not overlap with the ranges of any other species of the *O. wappesi* species group.

Material Examined

We have seen the type series of *O. pacifica* only; see above for details.

The *aeneipennis* Species Group

Diagnostic Combination

With character states of *Onypterygia*, restricted as follows. Adults of this species group are small in size (TL ca. 7–9 mm); head dorsally and pronotum piceous to black, with hint of green; elytra metallic green or blue, with or without cupreous reflection. Pronotal setae two pairs, each elytron with three discal setae in or near interval 3, hind femur without dorsoapical setae, abdominal sterna IV–VI each with one pair of ambulatory setae, and abdominal sternum VII with one pair of posterior marginal setae in males, and two pairs in females. Pronotum (Fig. 34–39) with lateral grooves narrow to moderately broad, lateral margins beaded posteriorly only, or not beaded, sinuate or not posteriorly; posterior pair of lateral setigerous punctures near posterolateral angles, slightly removed from margins, not on bead. Metathorax of average size, not short, metepisternum distinctly longer than wide. Elytral apex rounded, not spined, and sutural apex not angulate or denticulate; interneurs about equally distinct, and preapical lateral calli absent.

Description

With character states of the *aeneipennis* species group, and the following. Body of average appearance, size moderate, measurements and proportions as in Table 2.

Color.—Body ventrally black to piceous; appendages rufopiceous to rufoflavous.

Microsculpture.—Head with microlines fine to effaced more or less extensively, mesh pattern iso-

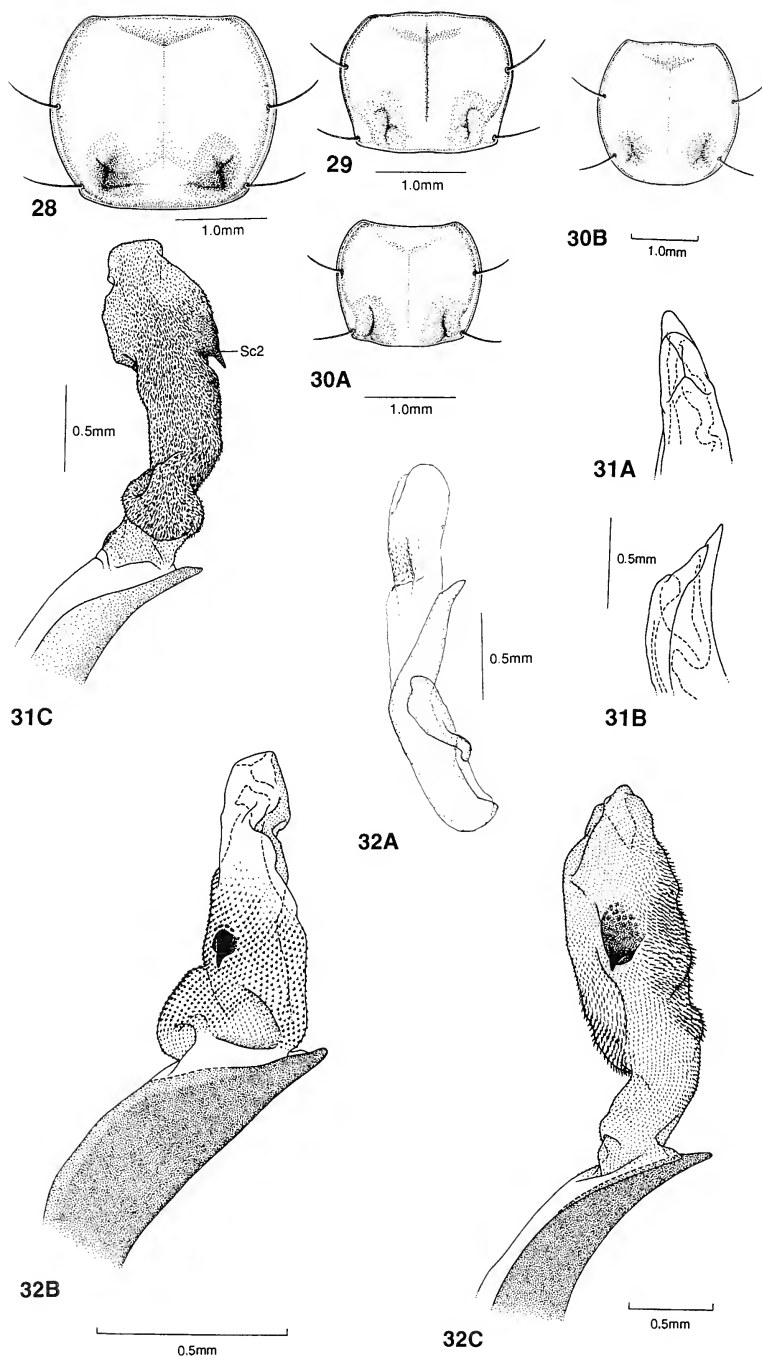


Fig. 28–32C.—Line drawings of adult structural features of the species of the *O. wappesi* species group. Fig. 28–30B, pronotum, dorsal aspect: 28, *O. wappesi*, n. sp.; 29, *O. amecameca*, n. sp.; 30A, *O. atoyac*, n. sp.; 30B, *O. shpeleyi*, n. sp. Fig. 31A–C, male genitalia, *O. wappesi*, n. sp.: A, B, median lobe, apical portion, dorsal and left lateral aspects, respectively; C, median lobe, left lateral aspect, with internal sac everted. Fig. 32A–C, median lobe, left lateral aspect, with internal sac everted: A, *O. pacifica*, n. sp.; B, *O. atoyac*, n. sp.; C, *O. shpeleyi*, n. sp. Legend: Sc1, Sc2—spinose sclerites 1 and 2, respectively.

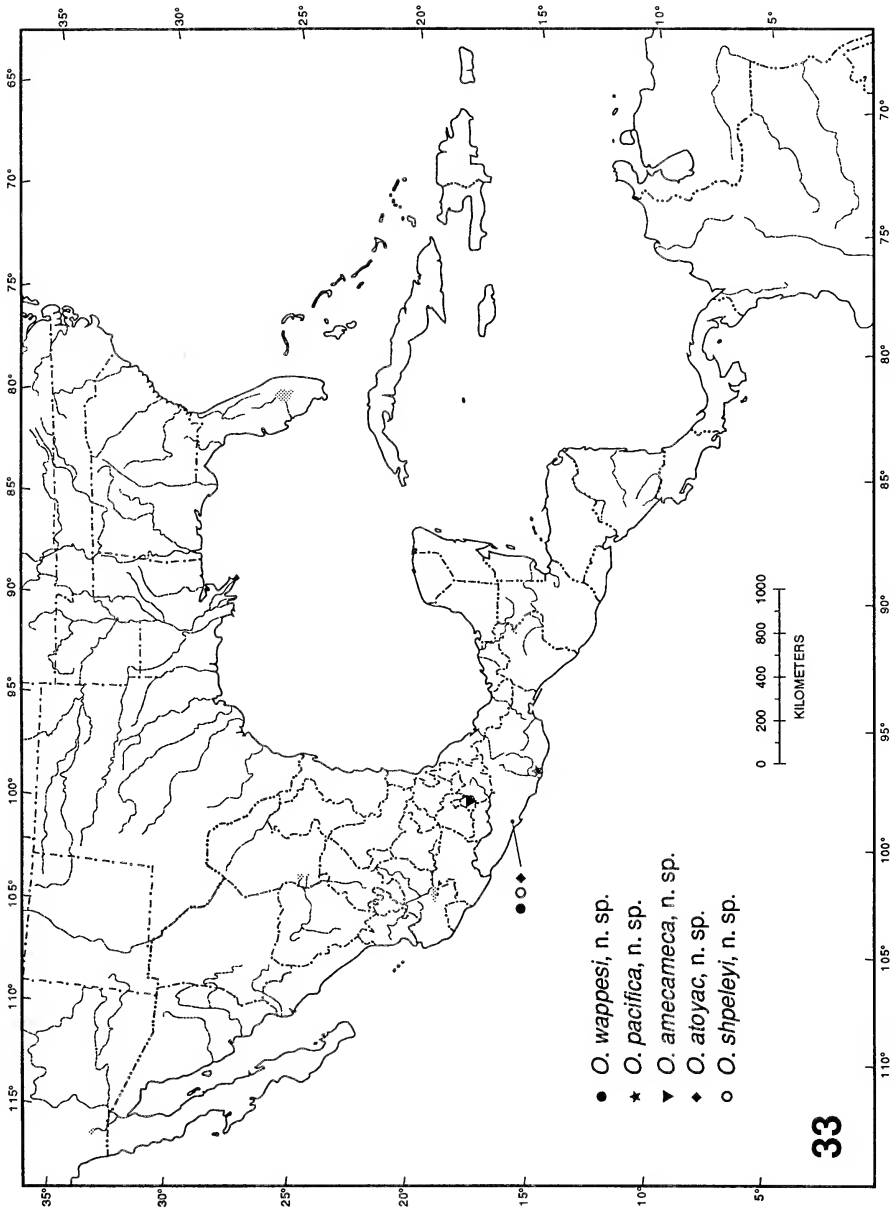


Fig. 33.—Map of southern North America, Middle, and northern South America, showing positions of collecting records for the species of the *O. wappesi* species group.

diametric or absent. Pronotum with microlines fine to effaced, mesh pattern transverse or absent. Elytra with microlines distinct, mesh pattern isodiametric to slightly transverse.

Luster.—Dorsal surface generally shining.

Head.—Frons and vertex smooth, without supraorbital carina each side.

Prothorax.—Pronotum (Fig. 34–39), surface sparsely punctate posterolaterally; posterolateral angles prominent to more or less obtuse. Prosternum with intercoxal process rounded apically.

Elytra.—Length moderate. Humeri developed fully, rounded. Lateral margins subparallel, slightly rounded. Discal and umbilical setigerous punctures not foveate. Interneurs 1 and 2 posteriorly of equal depth on apical declivity.

Hind Wings.—Macropterous, with membrane infuscated, wedge cell elongate, triangular, short sides equal to one another; or brachypterous.

Legs.—Tarsomeres 2–4 with climbing setae ventrally markedly dense (cf. Fig. 11G:cs). Tarsomere 5 with ventrolateral setae normally developed (cf. Fig. 11G:vs). Claws with pectinations more extensive (cf. Fig. 11H:p).

Male Genitalia.—Median lobe (Fig. 40–45) with apical portion short, triangular, apex narrow; internal sac (Fig. 40C; 41B; 42C; 44C, D; 45) with two spinose sclerites, one basal and one medial, located variously about circumference of internal sac; without basal and preapical lobes.

Ovipositor.—Stylomere 2 as in Figure 14, form 1, falcate, with seven or eight lateral ensiform setae, not restricted to dorsolateral margin.

Taxonomic Notes

All taxa included in this species group are allopatric in relation to one another. They seem to comprise a geographical mosaic entity, and may represent conspecific geographical vicars rather than distinct species. Some samples are brachypterous, others wing-dimorphic, and others macropterous. The metepisternum remains much longer than wide, but is shortened slightly in some populations, and the length of the metasternum between hind and middle coxae is much more than half the length of the hind coxa.

Nearly all geographic samples examined are distinctive, such that possible taxonomic solutions to the group ranged from one geographically varied species to numerous allopatric species. We chose a conservative resolution: since four taxa were named already, we recognize these as valid, and distinguish two others that seem equally distinct. However, since these taxa might be treated by others as subspecies, we discuss them together.

Pronotal variation is extreme. Some samples from the Transvolcanic Sierra (*O. pallidipes*, *O. stenapteryx*) and Sierra Madre del Sur (*O. aeneipennis*, *O. cupricauda*) tend to have markedly sinuate lateral margins and sharp posterolateral angles. Other samples from the Transvolcanic Sierra (*O. rubida*) and from various localities in the Sierra Madre Oriental and northern slopes of the Sierra Madre del Sur (*O. batesi*) have the lateral margins barely sinuate and posterolateral angles more obtuse. The pronotal base is notably rounded at sides in specimens from the Sierra Madre Oriental. The width of the lateral grooves varies markedly, from quite narrow in western forms (*O. aeneipennis*, *O. cupricauda*, *O. stenapteryx*) to moderately broad in central and eastern taxa (*O. pallidipes* and *O. rubida*, and Sierra Madre Oriental samples of *O. batesi*), and particularly broad in Oaxaca samples of *O. batesi*.

Pterothoracic variation is exhibited by metasternum and metepisternum, by form of elytra, and by development of the hind wings: macropterous specimens have normally developed humeri and a more elongate metepisternum and metasternum; brachypterous specimens have ovate elytra, or at least humeri reduced, and metasternum and metepisternum slightly shortened. *Onypterygia pallidipes* is macropterous, and most specimens have been collected by beating or at lights, at night. The other species are brachypterous or wing-dimorphic, are much less com-

monly collected, and because many specimens have been collected on the ground, the species may be primarily terricolous.

Among the taxa with markedly sinuate lateral pronotal margins, *O. aeneipennis* and *O. cupricauda* seem most similar to *O. stenapteryx*. *Onypterygia pallidipes* is paler (the wider margins of the pronotum, at least, are rufous), but the Uruapan specimen of *O. stenapteryx* also is somewhat pale. If these four nominal forms were assumed to be conspecific, the continuum would be from Oaxaca to Guerrero (medial spinose sclerite of internal sac ventral) to Michoacán to Mexico (spinose sclerite left lateral) to Cuernavaca (spinose sclerite right mediodorsal).

The taxa with slightly sinuate lateral pronotal margins (*O. rubida* and *O. batesi*) are neither proximal nor similar to one another. *Onypterygia rubida* is most similar to *O. pallidipes* although apparently more proximal geographically to *O. stenapteryx*, whereas *O. batesi* is more similar to *O. aeneipennis* and *O. cupricauda* than to the taxa in the Transvolcanic Sierra. The latter similarity involves primarily features postulated to be plesiotypic.

Habitat

The species of the *aeneipennis* group occur in mesic oak, oak–*Liquidambar*, and oak–pine forest, from about 1000 to 2600 m altitude.

Geographical Distribution

The range of this group is confined to central Mexico south of the Tropic of Cancer, extending from the Sierra Madre Oriental in the east, through the Transvolcanic Sierra to the Sierra Madre del Sur on the Pacific Versant (Fig. 46).

Chorological Affinities

See “Chorological Affinities” section for *famini* group above.

Included Species

The *aeneipennis* species group includes six allopatric species: *O. batesi*, n. sp.; *O. aeneipennis* Chaudoir; *O. cupricauda* Casey; *O. stenapteryx*, n. sp.; *O. pallidipes* Chaudoir; and *O. rubida* Bates.

Onypterygia batesi, new species

(Fig. 13A, B; 34; 40A–C; 46)

Type Material

Sixteen specimens. Holotype male, labelled: “MEX. TAMAULIPAS/Rancho del Cielo/3800', 8 mi. w./Gomez Farias/July 24–29, 1971”; “George E. and Kathleen E. Ball/collectors” (USNM). Allotype female, labelled same as holotype. Fourteen additional paratypes. Male, female, labelled same as holotype. Female, labelled: “MEX. Tamaulipas/Sierra de Guate-/mala, Rancho del/Cielo, 8 mi. n.w./Gomez Farias, 3800' X.6–10.65”; “G. E. Ball/D. R. Whitehead/collectors” (UASM). Three females, labelled: “MEX. S.L.P./24.7 mi. e. Landa/ de Matamoros/ Qro. 9000'/X.18–19.65”; “George E. Ball/D. R. Whitehead/collectors” (BMNH, CUC, MNHP). Male, labelled: “MEX. QRO. 21.8 km e./Landa de Matamoros/oak, arroyo; 1400 m/20.VIII.1985 63-85”; “MEXICAN EXP. 1985/H. E. Frania & D. Shpeley/collectors” (BMNH). Male, two females, labelled: “MEXICO: Hidalgo/rte. 105, 7.7 km S/Tlanchinol/20 July 1988/R. Turnbow” (RHTC). Male, labelled: “MEXICO: Hidalgo/3.4 km N Tlanchinol/ 21 July 1988/R. Turnbow” (RHTC). Female, labelled: “MEX. Oaxaca/Rte. 190 33.0 mi/n.w. Oaxaca/oak forest/Sept. 4–5, 1967; Ball, T. L. Erwin/R. E. Leech/collec-

tors" (CASC). Female, labelled: "MEX. Oaxaca/Cerro Zempoaltepetl/7200' (below Tla-huitoltepec)/creek side/August 21, 1972"; "B. S. Heming/G. E. Ball/collectors" (UASM). Female, labelled: "MEX: Veracruz/Las Minas Rd. 10 km/N. Rte 140 29 Jul/1990 el. 1875 m"; "beating/J. K. Liebherr" (CUIC).

Type Locality

Rancho del Cielo, Sierra de Guatemala, near Gómez Farías, Tamaulipas, Mexico.

Specific Epithet

Latinized genitive form of the surname of Henry Walter Bates; in recognition of his extensive studies of the Neotropical Carabidae.

Diagnostic Combination

With character states of *O. aeneipennis* species group, restricted as follows. Femora infuscated; elytra metallic green with evident cupreous reflections laterally, humeri rounded; brachypterous or macropterous; internal sac with distal sclerite ventral; and pronotum moderately broad to broad (LP/WP 0.83–0.94), base moderately to markedly rounded laterally, lateral margins not markedly sinuate before bluntly obtuse posterolateral angles, not beaded, lateral grooves broad, and anterior seta removed from adjacent margin by ca. 1.5–3.0 width of puncture. Adults of this species and *O. pallidipes* differ in that the latter has markedly sinuate pronotal margins (Fig. 38) and noncupreous elytra. In Oaxacan specimens of *O. batesi*, the wide pronotum differs markedly from the narrow pronotum characteristic of *O. aeneipennis*.

Description

With diagnostic character states of *O. batesi* and the following.

Measurements and Proportions of Holotype.—TL small (7.4 mm), WP/WH intermediate (1.36), LP/WP intermediate (0.91), WP/WPb intermediate (1.24), LE/WE low (1.60).

Color.—Antennae with basal and apical articles rufous. Palpi rufopiceous. Pronotum dark green. Femora rufopiceous; tibiae and tarsi rufous.

Prothorax.—Pronotum (Fig. 34). Anterior bead complete. Posterolateral impressions impunctate, or sparsely punctate; angles broadly rounded.

Pterothorax.—Mesepisternum impunctate to generally punctate.

Elytra.—Interneurs 2–6 continuous, shallow, punctate for part of length.

Hind Wings.—Dimorphic: macropterous or brachypterous.

Legs.—Tarsomeres 1–2 of mid- and hind tarsi sulcate. Fore tarsomere 4, inner lobe longer than basal portion; hind tarsomere 4, outer lobe as long as basal portion.

Male Genitalia.—Median lobe as in Figure 40A, B. Internal sac (Fig. 40C), armature two spinose sclerites, basal spine dorsal, medial spine ventral.

Ovipositor.—Stylomere 2 as in Figure 13A, B.

Habitat

Most specimens of this species were taken in terrestrial or creek margin habitats in mesic oak or oak–*Liquidambar* forest, from 1150 to 2200 m altitude, from June through November.

Geographical Distribution

This species is known in Mexico from the eastern slopes of the Sierra Madre Oriental, the Transvolcanic Sierra, and Atlantic drainages in Oaxaca (Fig. 46).

Chorological Affinities

This species, the only member of the *aeneipennis* species group from Atlantic drainages of the Mexican highlands, is not known to be sympatric with any other members of this group. The most proximal member of the *aeneipennis* group in the Transvolcanic Sierra is *O. pallidipes*.

Material Examined

We have seen the type series of *O. batesi* only; see above for details.

Onypterygia aeneipennis Chaudoir (Fig. 35; 41A, B; 46)

Onychopterygia aeneipennis Chaudoir (1878:276). Type material: three females, from Oaxaca, Mexico.

Lectotype (here designated): first of the three specimens; labelled "Ex Musaeo Chaudoir", Chaudoir-Oberthür collection (MNHP).

Onypterygia aeneipennis; Bates, 1882:132.

Type Locality

The type area is "Oaxaca." We restrict the type locality to Santa Catarina Juquila, Oaxaca, Mexico, located on the Pacific Versant of the Sierra Madre del Sur.

Diagnostic Combination

With character states of *O. aeneipennis* species group, restricted as follows. Elytra metallic green with evident cupreous reflections; pronotum narrow (LP/WP 0.95 or more), base moderately rounded laterally, lateral margins markedly sinuate before sharp, nearly right posterolateral angles, beaded posteriorly only, and lateral grooves narrow, with anterior seta removed from margin by about the width of its setigerous puncture; humeri oblique, and hind wings brachypterous. Additionally, males are recognized by the ventral position of the medial sclerite of the internal sac (Fig. 41B).

The pronotum in *O. aeneipennis* adults is much narrower (LP/WP 0.98, two specimens) than in adults of geographically proximal *O. batesi* in Atlantic drainages of Oaxaca (LP/WP 0.83–0.84, two specimens) and *O. cupricauda* in Pacific drainages of Guerrero (LP/WP 0.86–0.89, five specimens). We judge that *O. aeneipennis* is neither sympatric nor continuous with those taxa.

Description

With character states of *O. aeneipennis* and the following.

Measurements and Proportions.—TL small (6.65 mm), WP/WH intermediate (1.36), LP/WP intermediate (0.98), WP/WPb intermediate (1.24), LE/WE low (1.56).

Color.—Head dark green. Antennae with basal and apical articles piceous-black. Palpi piceous. Pronotum dark green. Elytra bright green. Femora, tibiae, and tarsi piceous-black.

Prothorax.—Pronotum (Fig. 35). Anterior bead complete; lateral beads present. Posterolateral impressions impunctate, or sparsely punctate; angles broadly rounded.

Pterothorax.—Mesepisternum partially punctate.

Elytra.—Interneurs 2–6 continuous, shallow, completely punctate.

Hind Wings.—Brachypterous.

Legs.—Tarsomeres 1–3 of mid- and hind tarsi sulcate. Fore tarsomere 4, inner lobe longer than basal portion; hind tarsomere 4, outer lobe shorter than basal portion.

Male Genitalia.—(Fig. 41A, B) Internal sac, armature (Fig. 41B). Enlarged microtrichia ventral.

Geographical Distribution

The range of this species is confined to the Pacific flanks of the southern part of the Sierra Madre del Sur (Fig. 46). A specimen from Omiltemi, Guerrero, (BMNH) was not examined critically, but may be a member of *O. cupricauda*.

Chorological Affinities

The range of *O. aeneipennis* is isolated from that of its nearest geographical neighbors, *O. batesi* and *O. cupricauda*.

Material Examined

In addition to type material and other specimens of *O. aeneipennis* from the type locality (BMNH and MNHP), we have seen the following, all collected in the Mexican state of Oaxaca.

1 male, 46.7 km S San Pedro Juchatengo, ca 1400 m, X.23.1966, Ray F. Smith (CISC); 1 male, Portillo del Sol, Jalatengo, X.21.1982, H. Brailovsky (CASC); 1 male, 2 females, 40.5 km S Suchixtepec, 1300 m, cloud forest, 92.027, VII.25.1992, R. S. Anderson (UASM).

Onypterygia cupricauda Casey

(Fig. 14; 36; 42A–C; 46)

Onypterygia cupricauda Casey (1920:224). Type material: two females (probably collected by Baron). Lectotype (here designated), female, labelled: "Guer"; "Casey bequest 1919"; "TYPE USNM 47569"; and "cupricauda Csy" (USNM). Paralectotype, female, labelled same as lectotype, except: "cupricauda-2 PARATYPE USNM 47569" (USNM).

Type Area

Guerrero, Mexico (probably near Chilpancingo).

Type Material

Both Casey specimens have apparently teneral coloration. The paralectotype is macropterous, with metepisternum normally developed and humeri broader than in the lectotype, has deeper interneurs, and its pronotum is relatively narrower anteriorly. As the legs of this specimen are relatively pale, the original description clearly was not based on this specimen.

Diagnostic Combination

With character states of the *O. aeneipennis* group, restricted as follows. Elytra metallic green, with marked metallic reflections; pronotum broad (LP/WP 0.86–0.89), base moderately rounded laterally, lateral margins only slightly sinuate before broadly rounded, obtuse posterolateral angles, lateral margins narrow, beaded posteriorly only, and anterior seta removed from margin by about width of its setigerous puncture; and humeri rounded, development average, and hind wings macropterous or brachypterous.

Description

With diagnostic combination of *O. cupricauda* and the following.

Measurements and Proportions.—TL small (8.0 mm), WP/WH intermediate (1.39), LP/WP intermediate (0.84), WP/WPb intermediate (1.25), LE/WE low (1.50).

Color.—Head dark green. Antennae with basal and apical articles rufopiceous. Palpi piceous. Elytra bright green. Femora piceous-black; tibiae and tarsi rufopiceous.

Prothorax.—Pronotum (Fig. 36). Anterior bead complete; lateral beads present. Posterolateral impressions densely punctate; angles broadly rounded.

Pterothorax.—Mesepisternum generally punctate.

Elytra.—Interneurs 2–6 continuous, shallow, punctate for part of length.

Hind Wings.—Dimorphic.

Legs.—Tarsomeres 1–3 of mid- and hind tarsi sulcate. Fore tarsomere 4, inner lobe as long as basal portion; hind tarsomere 4, outer lobe shorter than basal portion.

Male Genitalia.—Median lobe as in Figure 42A, B. Internal sac (Fig. 42C), armature two spinose sclerites, median spinose sclerite ventral, preapically and medially with field of slightly enlarged microtrichia.

Ovipositor.—(Fig. 14) For details see description of this feature for the *aeneipennis* species group.

Habitat

Cloud forest, in vegetation and leaf litter.

Geographical Distribution

This species is known only from montane localities on the Pacific slopes of the Sierra Madre del Sur, in Guerrero (Fig. 46). A specimen in BMNH, from Omiltemi, Guerrero, and not examined critically by us, probably belongs to this species.

Chorological Affinities

This species is not known to be sympatric with other members of the *O. aeneipennis* species group, but it is sympatric and perhaps syntopic with *O. wappesi* of the *O. wappesi* species group.

Material Examined

In addition to the type specimens, we have seen 18 specimens from the following localities, all in the state of Guerrero, Mexico.

Nine males, 5 females, 71 km SE Atoyac de Alvarez, cloud for., beating vegetation, 1700 m, 28-92, VII.25.1992, D. Shpeley (UASM); 1 male, same locality as above, but collected in tree fall leaf litter, J. S. Ashe (UASM); 1 male, 26 km NW El Paraíso, 1800 m, VIII.9.1986, Rawlins/Davidson (CMNH); 1 male, 1 female, 10 Km WSW Xochipala, 1650 m, VI.30.1982, J. E. Rawlins (CMNH).

Onypterygia stenapteryx, new species

(Fig. 18, 37, 43A–C, 46)

Type Material

Ten specimens. Holotype male, labelled: "MEX. Michoacán/18.8 mi. w. Uruapan/creek margin/7200'/August 15, 1967"; "Ball, T. L. Erwin/R. E. Leech/collectors" (USNM). Allotype female, labelled: "Tancitaro, Michoacan,/MEXICO alt. 6000 ft./June 25 1941 under moss"; "coll H. Hoogstraal"; "Colpodes/sp./det. Val 1942" (USNM). Additional paratypes nine, labelled as follows. Male, "Temascaltepec/Mex. D. F. 1931/G. B. Hinton"; "Van Dyke Collection" (CASC). Two females, "Temascaltepec/1931 Mex. D. F."; G. B. Hinton/Collector"; "Van Dyke/Collection" (CASC). Male, "Bejucos, Mex./Temescaltepec"; "H. E. Hinton/Collector" (MCZC). Male (tips of elytra and terminal abdominal segments missing), "Real de Arriba/Temascaltepec/Mex. VII.1932" (CASC). Female, "MEX: Mich. 14.3 km S/Uruapan, 1370–1465 m/29.vii.88/R. S. Anderson/oak-acacia woodland 88-10" (UASM). Female, "2 mi. NE Ixtapan/de la Sal, Mex., MEX. VII-18-1974/R L Mangan &/D S Chandler" (FSCA). Male, "Harry Brailovsky Col./MEXICO/Halinalco/Edo. de Mé-/xico/19-XI-80"; "Colección del Instituto/de Biología, UNAM./Mexico, D. F."; "♂ gen. drawn/D. Hollingdale/1991" (CASC). Female, "MEX. Mich. 97.7 km/w Apatzingán on rd/to Dos Aguas litter pine-oak; 1700 m/8.VIII.1985 37-85"; "MEXICAN EXP. 1985/H. E. Frania &/D. Shpeley/collectors" (UASM).

Type Locality

30.2 km west of Uruapan, state of Michoacán, Mexico.

Specific Epithet

Derived from two Greek words, *stenos* and *pteryx*, meaning narrow winged, with reference to the narrow elytral humeri.

Diagnostic Combination

With character states of the *O. aeneipennis* species group, restricted as follows. Femora rufous to rufopiceous, and elytra metallic green with cupreous reflections; pronotum broad to narrow (LP/WP 0.85–0.96), base moderately rounded laterally, lateral margins moderately to markedly sinuate anterad sharply obtuse postero-lateral angles, lateral margins narrow, beaded posteriorly only, and anterior seta removed from margin about 1.0–1.5 width of its setigerous puncture; elytral humeri oblique, hind wings brachypterous. Further, males are distinguished by the left-lateral position of the medial spinose sclerite of the internal sac.

Description

With diagnostic character states of *O. stenapteryx* and the following.

Habitus.—As in Figure 18.

Measurements and Proportions of Holotype.—TL small (6.62 mm), WP/WH intermediate (1.28), LP/WP intermediate (0.93), WP/WPb intermediate (1.28), LE/WE low (1.52).

Color.—Head dark green. Antennae with basal and apical articles rufous. Palpi rufopiceous. Elytra bright green. Femora piceous-black; tibiae and tarsi rufopiceous.

Prothorax.—Pronotum (Fig. 37). Anterior bead complete; lateral beads present. Posterolateral impressions impunctate, or sparsely punctate; angles obtuse.

Pterothorax.—Mesepisternum impunctate, or partially punctate.

Elytra.—Interneurs 2–6 continuous, moderately deep, or shallow; impunctate, or punctate for part of length.

Hind Wings.—Brachypterous.

Legs.—Tarsomeres 1–3 of middle tarsi sulcate; tarsomeres 1–2 of hind tarsi sulcate. Fore tarsomere 4, inner lobe longer than basal portion; hind tarsomere 4, outer lobe shorter than basal portion.

Male Genitalia.—Median lobe as in Figure 43A, B. Internal sac (Fig. 43C) with enlarged microtrichia few, ventral.

Variation

The Uruapan specimen, which seems to be fully mature, is paler than other specimens. The Ixtapan specimen has bluish elytra, clearly green and with cupreous reflections only near apex. Pronotal form varies considerably: LP/WP 0.92 at Ixtapan, 0.88–0.96 at Temascaltepec, 0.93 at Uruapan, 0.85 at Apatzingán, and 0.86 at Tancítaro. The Tancítaro specimen has the lateral margins of the pronotum less markedly sinuate and posterolateral angles more obtuse.

Habitat

Specimens have been collected on the ground in pine–oak litter, along a creek margin, and in moss. The known altitudinal range is from 1700 to 2200 m.

Geographical Distribution

This species is known from the southern fringes of the Transvolcanic Sierra in the central Mexican states of México and Michoacán (Fig. 46).

Chorological Affinities

Known localities of *O. stenapteryx* are on portions of the Río Balsas system that drain the southern slopes of the Transvolcanic Sierra. Other taxa in the *O. aeneipennis* species group that therefore may be continuous or sympatric with *O. stenapteryx* are *O. rubida* and *O. pallidipes*.

Material Examined

We have seen the type series of *O. stenapteryx* only; see above for details.

Onypterygia pallidipes Chaudoir (Fig. 38, 44A–D, 46)

Onychopterygia pallidipes Chaudoir, 1878:276. Holotype male, labelled: "TYPE/H.T." [circular, ringed with red]; "Puebla"; "Mexico/ Sallé Coll."; "614"; "Type"; "B.C.A. Col.I.1/ Onypterygia / pallidipes./ Chaud"; "Onypterygia/ pallidipes/ Chaud/ Puebla" [handwritten]; "Onychopterygia/ pallidipes Chaud/ apud Sallé" [handwritten]; "Holo-/ type" [circular, ringed with red]; ♂ BMNH/HOLOTYPE/ det. D. R. Whitehead/ Onypterygia/ pallidipes/ Chaudoir/ det. D. R. Whitehead" (BMNH).

Onypterygia pallidipes; Bates, 1882:132.

Type Material

Chaudoir (1878:276) records but a single specimen of this species, from the collection of A. Sallé. Thus, we infer that, in the absence of a specimen of this

species in the MNHP from the Sallé Collection, the one noted above must be the one on which Chaudoir based his description.

Diagnostic Combination

With character states of the *O. aeneipennis* species group, restricted as follows. Pronotum with lateral margins pale, femora rufous, and elytra rufescent with metallic green or blue cast but with little or no apical cupreous reflections; pronotum moderately broad (LP/WP 0.83–0.92), base straight laterally, lateral margins markedly sinuate anterad obtuse to acute posterolateral angles, lateral margins broad, not beaded, and anterior seta removed from side margin by about 2.0 width of its setigerous puncture; humeri broadly rounded, and hind wings macropterous. Further, males are distinguished by the medial spinose sclerite of internal sac being right mediodorsal in position.

Males are similar to those of *O. rubida* in lacking cupreous elytral color and by having the medial sclerite of the internal sac dorsal, but differ from that species by the markedly sinuate lateral margins of the pronotum and by the acute posterolateral angles. In elytral color, a specimen of *O. stenapteryx* from the geographically proximate locality of Ixtapan de la Sal is transitional in elytral color to *O. pallidipes*.

Description

With diagnostic character states of *O. pallidipes* and the following.

Measurements and Proportions.—TL small (7.45 mm), WP/WH intermediate (1.33), LP/WP intermediate (0.92), WP/WPb intermediate (1.22), LE/WE low (1.47).

Color.—Head dark green. Antennae with basal and apical antennomeres rufotestaceous. Palpi testaceous. Elytra bright green. Femora, tibiae, and tarsi rufotestaceous.

Prothorax.—Pronotum (Fig. 38). Anterior bead complete; lateral beads absent. Posterolateral impressions impunctate, or sparsely punctate; angles acute.

Pterothorax.—Mesepisternum impunctate, or partially punctate.

Elytra.—Interneurs 2–6 continuous, shallow; impunctate, or punctate for part of length.

Hind Wings.—Macropterous.

Legs.—Tarsomeres 1–3 of middle tarsi sulcate; tarsomeres 1–2 of hind tarsi sulcate. Fore tarsomere 4, inner lobe longer than basal portion; hind tarsomere 4, outer lobe shorter than basal portion.

Male Genitalia.—Median lobe as in Figure 44A, B. Internal sac (Fig. 44C, D) moderately long; enlarged microtrichia ventral.

Habitat

This species lives in tropical deciduous and oak forests, at altitudes between 1400 and 2100 m. Adults have been collected in June, July, and August: at night, at UV light traps, and in daytime by beating low vegetation.

Geographical Distribution

This species occurs on the southern edge of the Transvolcanic Sierra of the central Mexican states of Morelos and Puebla (Fig. 46).

Chorological Affinities

This species is not known to be sympatric with others of the *O. aeneipennis* species group, but may be continuous with *O. stenapteryx* and *O. rubida*, which also live on the southern slopes of the Transvolcanic Sierra drained by the Río Balsas.

Material Examined

In addition to the type specimen, we have seen approximately 25 specimens of *O. pallidipes* in total. All localities are in Mexico.

Morelos: Cuernavaca (UASM); 7 and 8.7 km E Cuernavaca (CASC, USNM, UASM). **Puebla:** 7 km SE Chipilo (UASM); Puebla (BMNH).

Onypterygia rubida Bates
(Fig. 39, 45, 46)

Onypterygia rubida Bates 1884:286. Type material: possible holotype, teneral male, H. W. Bates—Oberthür Coll. (MNHP).

Type Locality

Pátzcuaro, Michoacán, Mexico.

Diagnostic Combination

With character states of the *O. aeneipennis* species group, restricted as follows. Pronotum with lateral margins pale, femora rufous, elytra rufescent with metallic blue or green cast, and no apical cupreous reflections; pronotum moderately broad (LP/WP 0.87–0.89), base nearly straight to moderately curved laterally, lateral margins very slightly sinuate anterad broadly to markedly obtuse posterolateral angles, lateral margins broad, beaded posteriorly only, and anterior seta removed from lateral margin by about 1.5–2.0 width of its setigerous puncture. Further, males are distinguished by the medial spinose sclerite of the internal sac being dorsal in position.

Description

With character states of *O. rubida*, and the following.

Measurements and Proportions.—TL small (7.42 mm), WP/WH intermediate (1.31), LP/WP intermediate (0.89), WP/WPb intermediate (1.25), LE/WE low (1.57).

Color.—Head rufopiceous. Antennae with basal and apical antennomeres rufotestaceous. Palpi testaceous. Pronotum rufopiceous. Elytra bright blue. Femora, tibiae, and tarsi rufotestaceous.

Prothorax.—Pronotum (Fig. 39). Anterior bead complete; lateral beads absent. Posterolateral impressions impunctate, or sparsely punctate; angles broadly rounded.

Pterothorax.—Mesepisternum impunctate, or partially punctate.

Elytra.—Interneurs 2–6 continuous, moderately deep, impunctate, or punctate for part of length.

Hind Wings.—Dimorphic.

Legs.—Tarsomeres 1–3 of middle tarsi sulcate. Tarsomeres 1–2 of hind tarsi sulcate. Fore tarsomere 4, inner lobe longer than basal portion; hind tarsomere 4, outer lobe shorter than basal portion.

Male Genitalia.—Internal sac moderately long, with enlarged microtrichia in broad mediopreapical band (Fig. 45).

Habitat

Adults have been collected on the ground, in pastures, in August, from altitudes of 2130 to 2590 m.

Geographical Distribution

This species is known from the Transvolcanic Sierra, from the Mexican states of Michoacán and Colima (Fig. 46).

Chorological Affinities

The range of this species may be continuous with those of *O. pallidipes* and *O. stenapteryx*, related species that also live on the southern slopes of the Transvolcanic Sierra drained by the Río Balsas.

Material Examined

In addition to the type, we have seen three specimens of *O. rubida*, all from Mexico, as follows.

Colima: 1 male, 5–10 km S Mazamitla, X.6.1992, J. E. Wappes (JEW). **Michoacán:** Huajumbaro (UASM); E Morelia (UASM); Pátzcuaro (BMNH).

The *perissostigma* Species Group

Diagnostic Combination

With character states of *Onypterygia*, restricted as follows. Adults of this species group are recognized readily by the very narrow, elongate body form (Fig.

19). Other features are: body size small (TL ca. 8 mm), color testaceous to rufotestaceous, elytra with metallic green reflection; frons and vertex each side with pronounced longitudinally directed carina; with two pairs of lateral pronotal setae, each elytron with three discal setae in or near interval 3, hind femur without dorsoapical setae, abdominal sterna IV–VI each with one pair of ambulatory setae, and sternum VII of males with one pair of posterior marginal setae, females with five to six pairs. Metepisternum distinctly longer than wide. Elytron with apex rounded, not spined, sutural apex not denticulate; surface without preapical lateral calli.

Description

With diagnostic combination of *perissostigma* species group, restricted as follows. Body slender, pronotum elongate, measurements and proportions as in Table 2.

Color.—Testaceous to rufotestaceous, head and pronotum with dorsal surfaces rufoaeneous, elytra with metallic green reflection; antennae, palpi, and legs testaceous.

Microsculpture.—Head and pronotum smooth, without microlines. Elytra with microlines fine, mesh pattern isodiametric.

Luster.—Dorsal surface generally shining.

Chaetotaxy.—Pattern indicated in “Diagnostic Combination” section above.

Head.—Eyes markedly convex, prominent.

Prothorax.—Pronotum (Fig. 47) with surface posterolaterally densely punctate, especially in and around posterolateral impressions; anterior bead complete, lateral margins sinuate posteriorly and narrowly beaded; lateral grooves narrow; posterior setigerous puncture each side close to distinct posterolateral angle, slightly removed from margin, not on bead. Prosternum with intercoxal process truncate apically.

Pterothorax.—Mesepisternum generally punctate. Metathorax normal size, metepisternum distinctly longer than wide.

Elytra.—Narrow, elongate. Elytron with humerus broadly rounded; lateral margin straight; discal and umbilical setigerous punctures not foveate. Interneurs 1 and 2 posteriorly, on apical declivity, of equal depth; interneurs punctate for part of length. For other details see “Diagnostic Combination” section above.

Hind Wings.—Macropterous, with wedge cell elongate, triangular, with short sides in length equal to one another.

Legs.—Tarsomeres 1–3 of middle and hind tarsi sulcate laterally. Fore tarsomere 4 with inner lobe longer than basal portion; hind tarsomere 4 with outer lobe longer than basal portion (Fig. 11C:l-4). Tarsomere 5 with ventrolateral setae thin, short, and few (Fig. 11D:vs); tarsomeres 2–4 with relatively few climbing setae (Fig. 11C). Tarsal claws with pectinations less extensive (Fig. 11E:p).

Male Genitalia.—Median lobe (Fig. 48) with apical portion short, apex narrow. Internal sac with one or more microtrichial fields, without basal and preapical lobes, setiform spines, and spinose sclerites.

Ovipositor.—Stylomere 2 form 1, falcate, with ca. 15–16 ensiform setae on dorsolateral margin and on lateral surface generally.

Habitat

The single included species is in montane tropical forest, at an altitude of 609 m. Although a locality as low as this one may seem hardly “montane,” according to the Holdridge system, vegetation formations in Middle America occurring as low as 500 m are classified as montane (Hartshorn, 1988). More specifically, the forest of the area in question was designated by Sarukhan (1968:14, fig. 4) as “Selva alta-mediana subperennifolia” and distinguished from lowland rain forest or “Selva alta perennifolia.” This distinction was not made by Rzedowski (1978: 159), who combined these forest types in one unit, designated “Bosque Tropical Perennifolio.” Because so few species of *Onypterygia* are known to enter true lowland tropical forest, we choose to follow the classifications of Hartshorn and Sarukhan rather than Rzedowski for characterization of habitats of this genus.

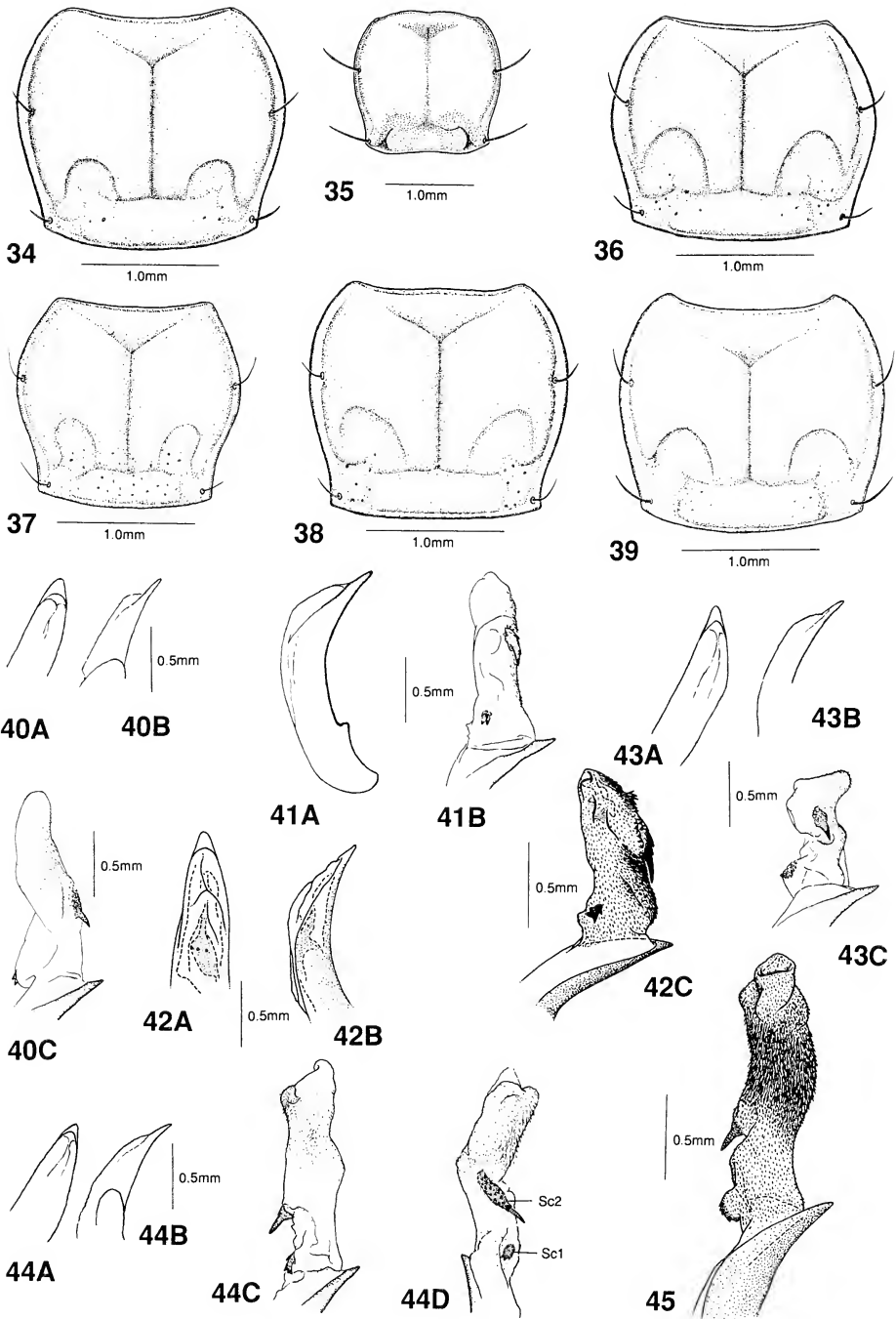


Fig. 34-45.—Line drawings of adult structural features of the species of the *O. aeneipennis* species group. Fig. 34-39, pronotum, dorsal aspect of: 34, *O. batesi*, n. sp.; 35, *O. aeneipennis* Chaudoir; 36, *O. cupricauda* Casey; 37, *O. stenapteryx*, n. sp.; 38, *O. pallidipes* Chaudoir; 39, *O. rubida* Bates. Fig. 40-45, male genitalia of: 40, *O. batesi*, n. sp.; A, B, median lobe, apical portion, dorsal and left lateral aspects, respectively. 41, *O. aeneipennis* Chaudoir, median lobe; A, left lateral aspect; B, median lobe, left lateral aspect. 42, *O. stenapteryx*, n. sp.; A, left lateral aspect; B, median lobe, left lateral aspect. 43, *O. cupricauda* Casey; A, B, median lobe, apical portion, dorsal and left lateral aspects, respectively; C, median lobe, left lateral aspect. 44, *O. pallidipes* Chaudoir; A, B, median lobe, apical portion, dorsal and left lateral aspects, respectively; C, median lobe, left lateral aspect. 45, *O. rubida* Bates, median lobe, left lateral aspect.

Geographical Distribution

This species is known from Mexico only, in central Oaxaca (Fig. 52).

Chorological Affinities

See "Chorological Affinities" section for the *famini* species group above.

Included Species

This group is monobasic, including only *O. perissostigma*, n. sp.

Onypterygia perissostigma, new species

(Fig. 11C–E; 19; 47; 48; 52)

Type Material

Four specimens. Holotype male, labelled: "2000', 6 mi. S./Valle Nacional,/Oax. Mex. V.18–20,/1971 H. Howden" (USNM). Allotype female, labelled same as holotype (USNM). Two additional paratypes, labelled as follows. Female, labelled same as holotype (BMNH). Female, "MEX. Oaxaca, 16.9/mi. S. Valle/Nacional 3600'/VIII.14–15.65"; "George E. Ball/D. R. Whitehead/collectors"; "pn drawn" (UASM).

Type Locality

9.7 km south of Valle Nacional, Oaxaca, Mexico.

Specific Epithet

Based on two Greek words, *perissos* and *stigma*, meaning oddly marked, in reference to the densely punctate pronotum as peculiar to this species.

Description

Habitus.—As in Figure 19.

Measurements and Proportions of Holotype.—TL small (7.50 mm), WP/WH high (1.04), LP/WP high (1.16), WP/WPb low (1.16), LE/WE high (1.96). See group description above for other details.

Pronotum.—As in Figure 47.

Legs.—Tarsal claws as in Figure 11C–E.

Male Genitalia.—As in Figure 48.

Variation

Paratypes vary in amount of genal rugosity; they are more fully matured than the holotype, and hence the elytra are darker beneath the metallic green luster.

Habitat

One of the paratypes (UASM) was collected near the margin of a temporary woodland pond in montane rain forest, as were specimens of *O. kathleenae*. Moth scales on their integument indicate that the holotype and other paratypes were collected at light.

Geographical Distribution

This species is known only from the eastern slopes of the continental divide, in central Oaxaca (Fig. 52).

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apical portion, with internal sac everted. 42, *O. cupricauda* Casey: A, B, median lobe, dorsal and left lateral aspects, respectively; C, internal sac everted, left lateral aspect. 43, *O. stenapteryx*, n. sp.: A, B, median lobe, apical portion, dorsal and left lateral aspects, respectively; C, internal sac everted, left lateral aspect. 44, *O. pallidipes* Chaudoir: A, B, median lobe, apical portion, dorsal and left lateral aspects, respectively; C, D, internal sac, everted, left and right lateral aspects, respectively. 45, *O. rubida* Bates: median lobe, apical portion, with internal sac everted. Legend: Sc1—spinose sclerite 1, Sc2—spinose sclerite 2.

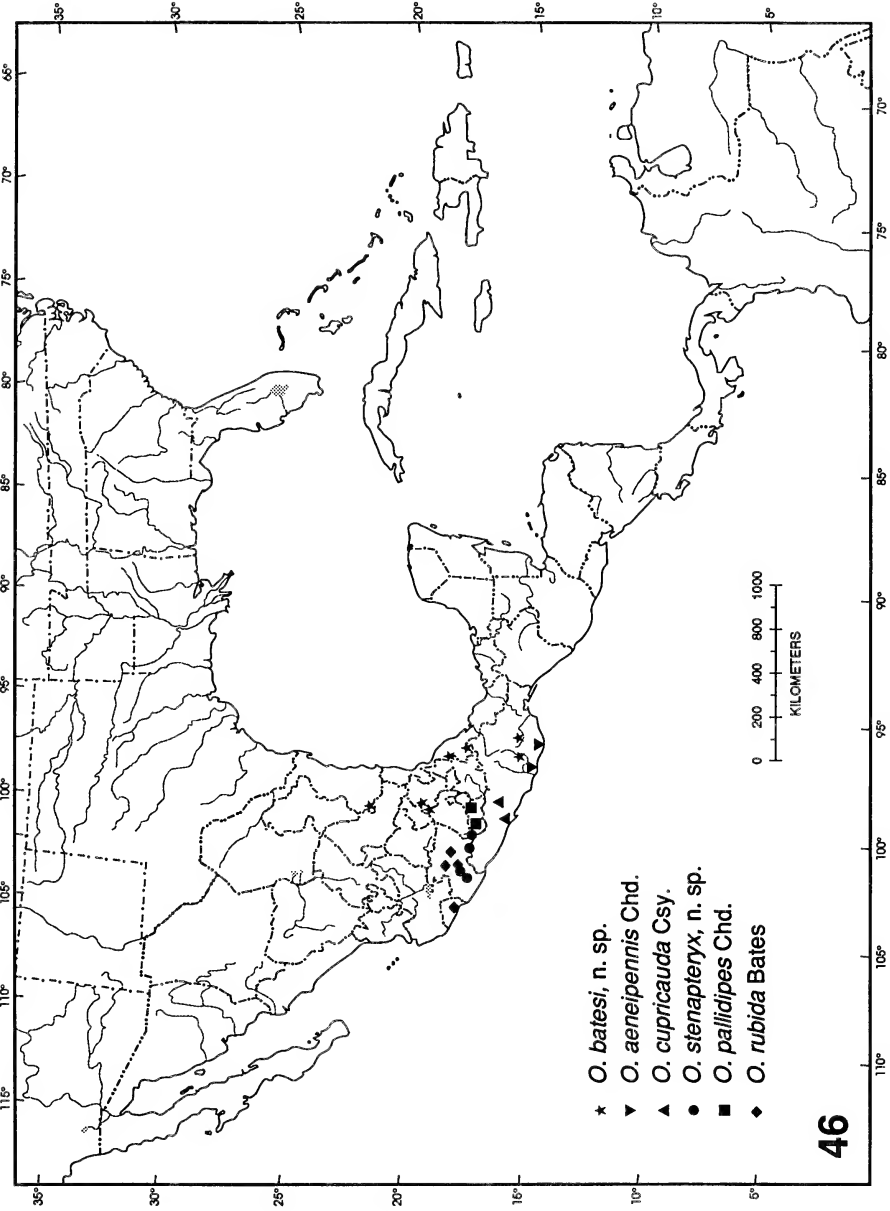


Fig. 46.—Map of southern North America, Middle, and northern South America showing positions of collecting records for the species of the *O. aeneipennis* species group.

Chorological Affinities

This species is sympatric with *O. kathleenae* in Oaxaca. Localities of *O. striblingi* and *O. exeuros* are in close proximity to that of *O. perissostigma*, so it seems likely that these species are sympatric. Also, the ranges of most other species groups overlap that of *O. perissostigma*, so one can expect reasonably that additional species will be sympatric with *O. perissostigma*.

Material Examined

We have seen the type material of *O. perissostigma* only; for details see above.

The *pusilla* Species Group

Diagnostic Combination

With character states of *Onypterygia*, restricted as follows. Adults of this species group are small (TL ca. 7–9 mm), head dorsally and pronotum piceous to black, elytra with disc concolorous, metallic green with cupreous reflection laterally to dark aeneous, with only a bare trace of color. Pronotal lateral setae two pairs, each elytron with three discal setae, in or near interval 3, hind femur without dorsoapical setae, abdominal sterna IV–VI each with single pair of ambulatory setae, and sternum VII of males with one pair of posterior marginal setae, females with two pairs. Elytral apex produced and angulate or denticulate (Fig. 49C), sutural apex rounded, interneurs about equally distinct, and preapical lateral elytral calli absent.

Description

With diagnostic combination of *pusilla* species group and the following. Body of average appearance, size moderate, measurements and proportions as in Table 2.

Color.—Body generally dark rufopiceous; palpi, tibiae, and tarsi paler, rufous; antennae with basal antennomeres piceous, apical antennomeres piceous to rufopiceous; elytra as noted in "Diagnostic Combination" section above.

Microsculpture.—Head nearly smooth, without microlines, or microlines very few and mesh pattern isodiametric. Pronotum with microlines very fine, surface nearly smooth, mesh pattern transverse. Elytra with microlines distinct, mesh pattern isodiametric.

Luster.—Dorsal surface shining.

Head.—Frons and vertex smooth, without supraorbital carina each side. Genae smooth, not rugose. Eyes moderately prominent, convexity average.

Prothorax.—Pronotum as in Figure 49A, B, sparsely punctate posterolaterally, posterolateral angles obtuse; anterior bead complete; lateral margins slightly sinuate posteriorly, beaded posteriorly only, lateral grooves moderately wide; posterolateral pair of setigerous punctures at posterolateral angles, slightly removed from margin, not on bead. Prosternum with intercoxal process rounded apically.

Pterothorax.—Mesepisternum partially punctate. Metathorax normal, metepisternum distinctly longer than wide.

Elytra.—Humeri broadly rounded; lateral margins slightly rounded, subparallel; discal and umbilical setigerous punctures deep, not foveate; interneurs 1 and 2 equally distinct posteriorly, on apical declivity; interneurs 2–6 continuous, moderately deep, punctate for part of length.

Hind Wings.—Macropterous, with membrane hyaline, not darkened; wedge cell elongate, triangular, with short sides equal to one another.

Legs.—Tarsomeres 1–3 of middle and hind tarsi sulcate. Fore tarsomere 4 with inner lobe longer than basal portion; hind tarsomere 4 with outer lobe shorter than basal portion. Tarsomeres 2–4 with climbing setae markedly dense (cf. Fig. 11F). Tarsomere 5 with ventrolateral setae normally developed (cf. Fig. 11D). Tarsal claws with pectinations more extensive (cf. Fig. 11H).

Male Genitalia.—Median lobe (Fig. 50A–E) with apical portion short, triangular, apex narrow; internal sac (Fig. 50C) without basal or preapical lobes; relatively short, with single basal spinose sclerite, or without spinose sclerites.

Ovipositor.—Stylomere 2 (cf. Fig. 51) form 1, falcate, with eight to ten ensiform setae on or near dorsolateral margin.

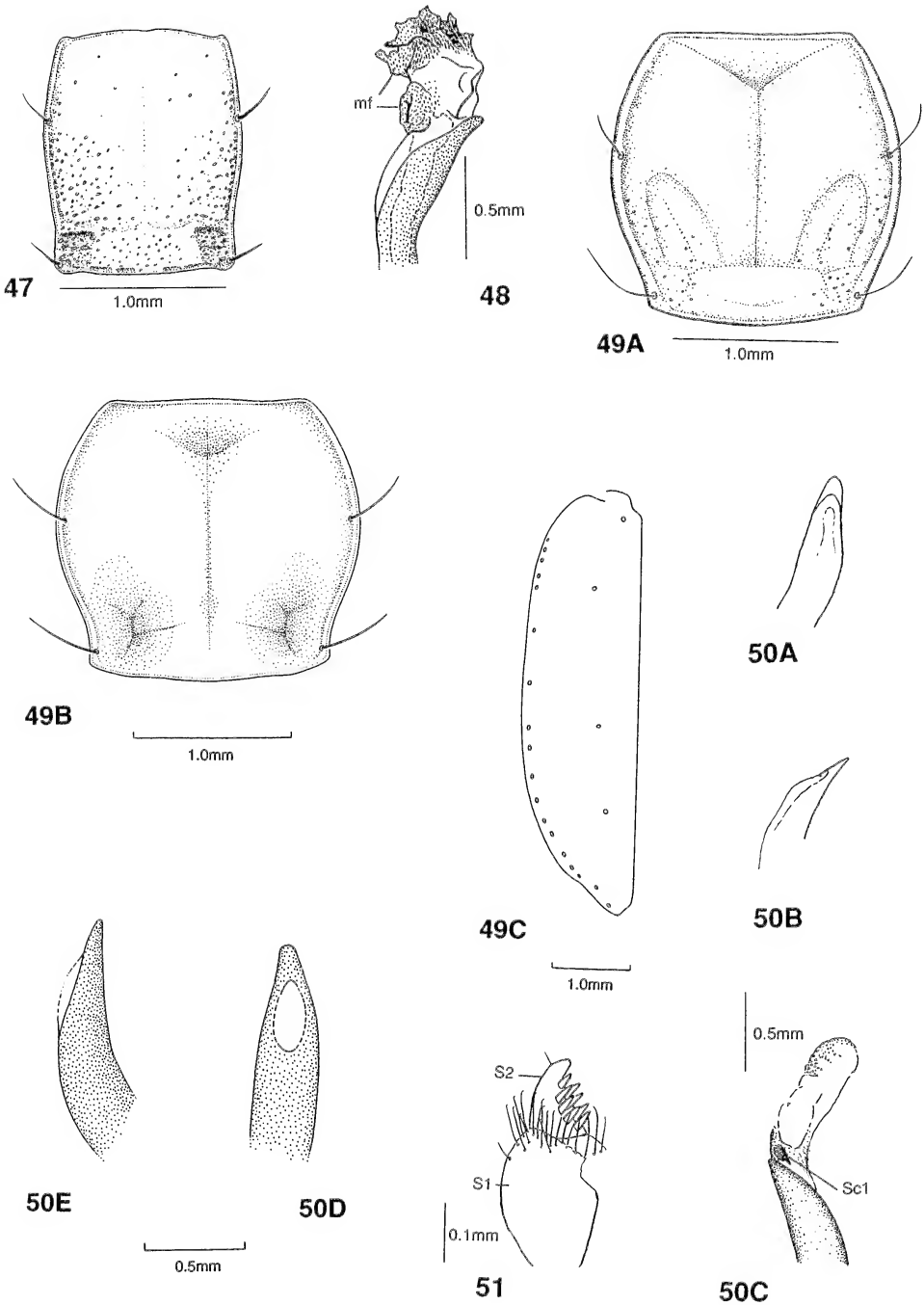


Fig. 47–51.—Line drawings of adult structural features of the *O. perissostigma* and *O. pusilla* species groups. Fig. 47, 49A, 49B, pronotum, dorsal aspect of: 47, *O. perissostigma*, n. sp.; 49A, *O. pusilla* Chaudoir; 49B, *O. rawlini*, n. sp. Fig. 49C, left elytron, dorsal aspect, of *O. rawlini*, n. sp. Fig. 48, 50, male genitalia: 48, *O. perissostigma*, n. sp., median lobe, apical portion, left lateral aspect, with internal sac everted; 50A–C, *O. pusilla* Chaudoir: A, B, median lobe, apical portion, dorsal and left

Habitat

The species of this group are known from tropical montane and oak–pine forests, between 700 and 1800 m altitude.

Geographical Distribution

The range of this species group is bicentric, with one species occurring on the Pacific Versant of Mexico in the southern part of the Sierra Madre Occidental and adjacent Transvolcanic Sierra, and another one farther south in the eastern Transvolcanic Sierra, Sierra Madre del Sur, and in the mountains of Chiapas and Guatemala (Fig. 52).

Chorological Affinities

See “Chorological Affinities” for *famini* group above.

Included Species

This group includes two species: *O. pusilla* Chaudoir, and *O. rawlinsi*, n. sp.

Onypterygia pusilla Chaudoir (Fig. 49A, 50A–C, 51, 52)

Onychopterygia pusilla Chaudoir 1878:276. Lectotype (here designated) male, with green Dejean labels “pusilla in Mexico” and “Orizaba”; also “Ex Musaeo Chaudoir” (Oberthür–Chaudoir Collection, Box 293/2/4, MNHP).

Onypterygia pusilla; Bates, 1882:133.

Type Material

In addition to the specimen noted above, Chaudoir (1878:277) referred to other specimens in the collection of Auguste Sallé, from Córdoba. These are designated paralectotypes.

Type Locality

Orizaba, Veracruz, Mexico.

Diagnostic Combination

With character states of *O. pusilla* species group, restricted as follows. Elytral apices angulate, color of elytra dull, nonmetallic to slightly metallic, and elytral interneurs relatively deeply engraved.

Description

With diagnostic combination of *O. pusilla* and the following.

Measurements and Proportions.—TL small (7.70 mm), WP/WH high (1.33), LP/WP intermediate (1.18), WP/WPb intermediate (1.21), LE/WE high (2.00).

Color.—Elytra metallic green with coppery reflections laterally. Legs with femora piceous-black; tibiae and tarsi rufopiceous.

Prothorax.—Pronotum (Fig. 49A).

Elytra.—Elytron, apex angulate to denticulate or acuminate.

Male Genitalia.—Median lobe as in Figure 50A, B. Internal sac (Fig. 50C), armature, one spinose sclerite.

Ovipositor.—Stylomere 2 as in Figure 51.

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lateral aspects, respectively; C, median lobe, apical portion, with internal sac everted; D, E, *O. rawlinsi*, n. sp., median lobe, dorsal and left lateral aspects, respectively. Fig. 51, ovipositor, stylomeres 1 and 2, lateral aspect, of *O. pusilla* Chaudoir. Legend: mf—microtrichial fields; S1, S2—stylomeres 1 and 2, respectively; Sc1—spinose sclerite 1.

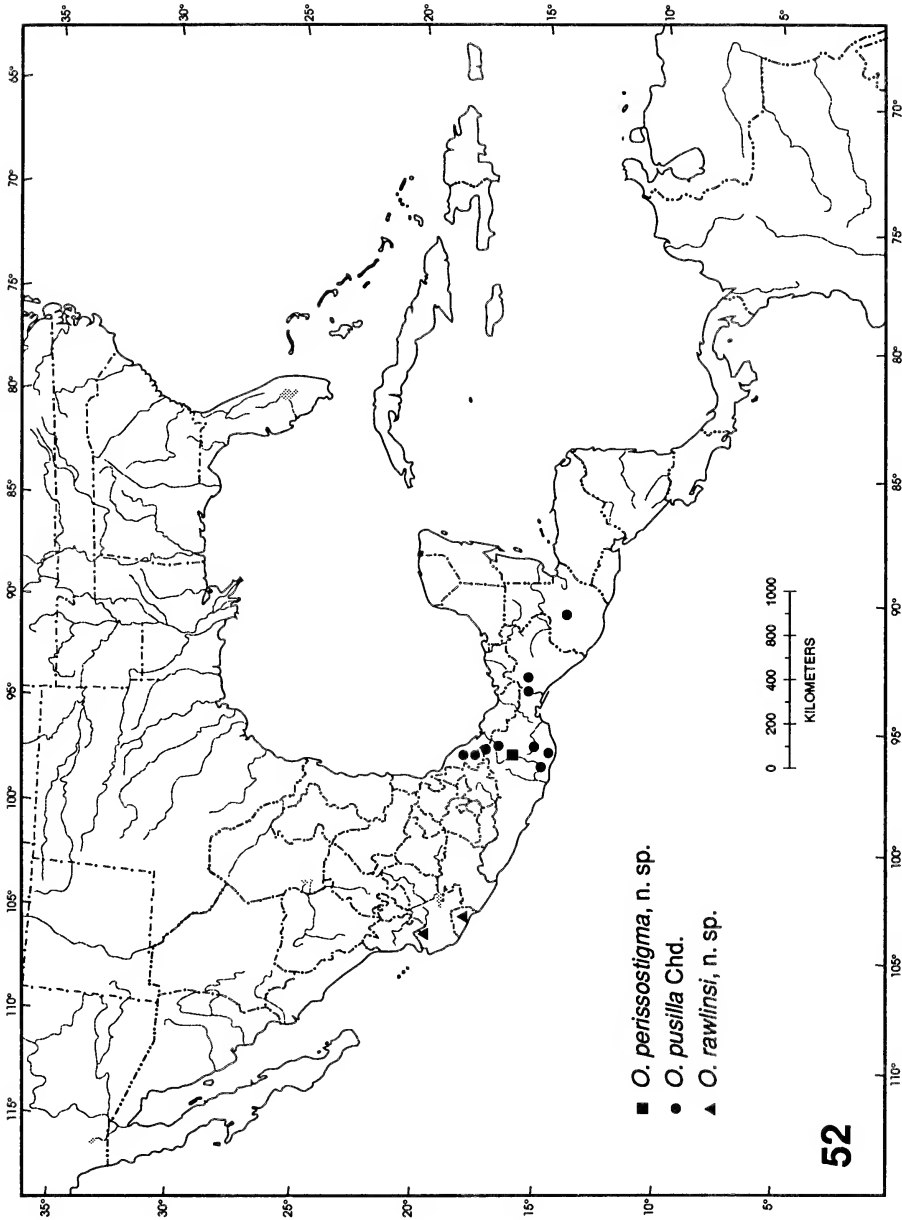


Fig. 52.—Map of southern North America, Middle, and northern South America showing positions of collecting records for the *O. perissostigma* and *O. pusilla* species groups.

Variation

A male from San Gabriel Mixtepec, Oaxaca, exhibits acuminate elytral apices, the projections almost as long and slender as those characteristic of *O. longispinis* Bates.

Habitat

Mexican specimens were collected in mesic woodlands at middle altitudes (884–1372 m): from bromeliads in March and December, at UV light traps in June, and by other methods from May through September.

Geographical Distribution

The range of this species extends from Guatemala northward in the west to the Sierra Madre del Sur in Oaxaca, and in the east to Jacala, in the state of Hidalgo (Fig. 52).

Chorological Affinities

This species is allopatric in relation to its closest relative, *O. rawlinsi*, n. sp. At Suchixtepec, Oaxaca, adults of *O. pusilla* were collected from bromeliads with adults of *O. angustata* and *O. hoepfneri*.

Phylogenetic Relationships

This species and *O. rawlinsi*, n. sp., are postulated to be adelphotaxa.

Material Examined

In addition to the type material we have seen approximately 70 specimens of *O. pusilla* from the following localities.

MEXICO. Chiapas: 10 km SW Ocosingo, 1067 m, VII.29.1966, Ball and Whitehead (UASM); 2 males, 10.3 km NW Ocosingo, 1069 m, oak–pine woodland, VII.19.1983, R. S. Anderson (UASM); 18.7 km N Ocozocoautla, 975 m, U–V light, VI.10–13.1966, Ball and Whitehead (UASM); Jct. Rts. 190 & 195, VI.11.1969, J. M. Campbell (CNCI). **Distrito Federal:** Mexico City. **Hidalgo:** 1 female, 46.7 km NE Jacala, 1371.6 m, V.27.1974, Marshall, C. W. & L. O'Brien (UASM); 1 female, 46.7 km NE Jacala 1372 m, V.27.1979, C. W. & L. O'Brien & B. Marshall (UASM). 46 km. SE Tamazunchale, 1494 m, VI.4.1975, Ball and H. E. Frania (UASM). **Oaxaca:** 1 specimen, 8 km S Candelaria Loxicha, VII.18–19.1974 (TAMU); 1 specimen, Juquila Mixes, V., H. F. Howden (CNCI); 3 males, Hwy. 131, 193 km S Oaxaca, 1463 m, V.12.1971, D. E. Bright (CNCI); 3 males, 1 female, Rte. 131, 187 km S Oaxaca, 1768 m, V.12.1971, J. M. Campbell (CNCI); Puerto Escondido Highway—52–58 km N Puerto Escondido (UASM); 1 specimen, 30.7 km S Suchixtepec, 1372 m, in bromeliads, Ball and Whitehead (UASM); 1 female, 11 km S Valle Nacional, 610 m, V.8.1971, D. E. Bright (CNCI); 2 males 3 females, 24 km S Valle Nacional, 1219 m, V.20.1971, D. E. Bright (CNCI); 5 specimens, 9.7 km S Valle Nacional, 610 m, V.18–20.1966, Ball and Whitehead (UASM); 1 specimen, 19.4 km S Valle Nacional, 914 m, V.17.1966, Ball and Whitehead (UASM); 1 specimen, 24 km S Valle Nacional, 1219 m, V.20.1966, Ball and Whitehead (UASM). **Veracruz:** 5 specimens, Córdoba (CASC); 8 specimens, same locality, VI.9–11, VII.8 (USNM); 1 specimen, Fortín de las Flores, 884 m, U–V light, V.27–28.1966, Ball and Whitehead (UASM); 6 km S Huatusco, 1370 m, cloud forest, bromeliads, VII.20.1978, G. E. and K. E. Ball (UASM); 1 female, Hwy. 140, 7.1 km N. Huatusco, 1300 m, beating weeds and vines, J. K. Liebherr, D. A. Millman (CUIC); Jalapa. 2 females, 1 km N. Jilotepec, 1300 m, beating, VII.31.1990, J. K. Liebherr (CUIC); Orizaba; 1 male, Río Metlac, 4 km S Fortín de las Flores, 900 m, VII.17.1990, J. K. Liebherr (CUIC). **GUATEMALA. Alta Verapaz:** 3 specimens, Panzós (BMNH, MCZC, Nègre Coll., MNHP); 1 female, San Cristóbal Quixal, V.1.1980, H. & L. Freude (ZSMC); 1 specimen, Senahú (BMNH). **Baja Verapaz:** 1 male, 7 km NE Purulhá, 1660 m, tropical montane forest, beating vegetation, 91-08, V.31.1991, Howden Exp., D. Shpeley, & K. E. & G. E. Ball (UASM).

Onypterygia rawlinsi, new species

(Fig. 49B; 50D, E; 52)

Type Material

Fourteen specimens, as follows. Holotype male, labelled: "23 km S Tepic,/ Nayarit MEXICO/3500' July 17,/1977 J. Rawlins" (CMNH). Allotype female and

additional paratypes (five males and five females) labelled same as holotype (CMNH, UASM). Two additional paratypes, labelled: male, "MEXICO Colima/ vic El Terrero/4 Oct 1992/R. Turnbow"; "Los Sauces rd./km mk. 1-2" (RHTC). Female, "MEXICO Colima W./Rd. to El Terrero/3-5000 ft. 3-5 Oct/1992 J. E. Wappes" (JEWG).

Type Locality

Mexico, state of Nayarit, 23 km south of Tepic.

Specific Epithet

This is the Latinized genitive form of the surname of the collector of most of the type series, John E. Rawlins, lepidopterist and Associate Curator, Section of Invertebrate Zoology, Carnegie Museum of Natural History, and named in recognition of and with gratitude for his enthusiastic efforts to improve knowledge of Neotropical Carabidae.

Diagnostic Combination

With character states of *O. pusilla* species group and, in addition to the distinctive combination of character states presented in the key, males of this species are recognized by absence of spinose sclerites from the internal sac of the genitalia. In size, form, and color, adults of *O. rawlinsi* are confused easily with those of the *O. aeneipennis* species group, but they differ in form of elytral apex: broadly rounded in the latter, obtusely angulate in the former.

Description

With diagnostic combination of *O. rawlinsi*, and the following. Body form and size average for the more primitive lineages of *Onypterygia*.

Measurements and Proportions of Holotype.—TL small (7.16 mm), WP/WH high (1.39), LP/WP intermediate (0.98), WP/WPb intermediate (1.32), LE/WE high (1.71).

Color.—Elytra aeneous. Legs, tibiae, and tarsi piceous to black.

Prothorax.—Pronotum as in Figure 49B.

Male Genitalia.—(Fig. 50D, E) Internal sac, armature absent.

Habitat

Probably rather dry oak-pine forest, to judge from the general vegetation cover in the areas where the specimens were collected. In fact, the specimens were taken at a light trap set "amid cornstalks at the edge of a small milpas . . ." and "the . . . forest nearby was disturbed secondary growth . . ." (John Rawlins, personal communication).

Geographical Distribution

This species is known only from the western slopes of the Sierra Transvolcanica in Mexico (Fig. 52).

Chorological Affinities

Specimens of this species were collected at the same time and in the same place as were specimens of *O. cyanea* and *O. hoepfneri*. This species is clearly isolated from the range of its putative adelphotaxon, *O. pusilla*, but it is overlapped by the species of the *O. aeneipennis* group, as well as being syntopic with the species noted above.

Phylogenetic Relationships

See this topic for *O. pusilla* above.

Material Examined

We have seen the type series of *O. rawlinsi* only; see above for details.

The *angustata* Species Group

Diagnostic Combination

With character states of *Onypterygia*, restricted as follows. Adults of this species group are small to intermediate in size (TL 7–11 mm), head dorsally and pronotum piceous to black, elytra with disc concolorous, metallic green, with cupreous reflection laterally, or completely cupreous. Pronotal lateral setae, one or two pairs, each elytron with three setae in or near interval 3, hind femur with or without dorsoapical setae, abdominal sterna IV–VI each with one pair of ambulatory setae, and sternum VII of males with one pair of posterior marginal setae, and females with two pairs. Elytral apex denticulate to acuminate (spinose), sutural apex angulate or rounded, interneur 1 more deeply impressed than other interneurs, and each elytron with a preapical lateral callus (Fig. 54C).

Description

With diagnostic combination of *angustata* species group, and the following.

Measurements and Proportions.—As in Table 2.

Color.—Body and appendages (except elytra) black to rufopiceous; see “Diagnostic Combination” section above for color of elytra.

Microsculpture.—Head with dorsal surface smooth, microlines absent, or mesh pattern partially effaced only, sculpticells isodiametric. Pronotum with surface nearly smooth, but microlines evident in small patches, mesh pattern transverse. Elytra with microlines fine, mesh pattern isodiametric.

Luster.—Dorsal surface shining.

Head.—Frons and vertex smooth, without supraorbital carina each side. Genae smooth, not rugose. Eyes moderately prominent, convexity average.

Prothorax.—Pronotum (Fig. 53; 54A, B), with surface smooth to densely punctate posterolaterally; posterolateral angles nearly rectangular; anterior margin with bead complete; lateral margins slightly sinuate posteriorly, beaded posteriorly only; lateral grooves moderately wide; posterolateral pair of setigerous punctures at posterolateral angles on or beside bead. Prosternum with intercoxal process rounded apically.

Pterothorax.—Mesepisternum impunctate to partially punctate. Metathorax normal, metepisternum distinctly longer than wide.

Elytra.—Moderately elongate. Elytron with humerus broadly rounded; lateral margin slightly rounded; discal setigerous punctures foveate or not; umbilical punctures foveate or not. Interneurs fine, interneur 1 posteriorly on apical declivity much deeper than interneur 2; interneurs 2–6 continuous, fine, punctate for part of length, or impunctate. Other details in “Diagnostic Combination” section, above.

Hind Wings.—(Fig. 55) Macropterous, wedge cell oblong, with short sides unequal to one another.

Legs.—Tarsomeres 1–2 or 1–3 of middle and hind tarsus sulcate laterally. Fore tarsomere 4 with inner lobe as long as or longer than basal part; hind tarsomere 4 with outer lobe shorter than, or as long as, basal portion. Climbing setae of tarsomeres 2–4 markedly dense (cf. Fig. 11F, G:cs). Tarsomere 5 with ventrolateral setae normally developed (cf. Fig. 11G:vs). Claws with pectinations more extensive (cf. Fig. 11H:p).

Male Genitalia.—Median lobe (Fig. 56–59) with apical portion short, triangular, apex narrow; internal sac (Fig. 56C, 57C, 59B) moderately elongate, without basal or preapical lobes, with basal spinose sclerite only, or with basal and median spinose sclerites.

Ovipositor.—Stylomere 2 (Fig. 60, 61) form 1, falcate, with four to ten ensiform setae on or near dorsolateral margin.

Habitat

The species of this group occupy mesic tropical montane to oak–pine forests, from about 600 to 1900 m altitude.

Geographical Distribution

The range of this group extends from Mexico south of the Tropic of Cancer to Panama and possibly to northern South America (Fig. 62).

Chorological Affinities

See “Chorological Affinities” for *famini* group above.

Included Species

Four species are included in this group: *O. longispinis* Bates; *O. angustata* Chevrolat; *O. pseudangustata*, n. sp.; and *O. sriblingi*, n. sp.

Onypterygia longispinis Bates

(Fig. 10, 56A–C, 62)

Onypterygia longispinis Bates, 1882:132. Lectotype (here designated) male on card with female, labelled "TYPE H. T."; "Cerro Zunil, 4–5000 ft. Champion"; "Onypterygia longispinis Bates" [handwritten]; "B.C.A. COL. I.1. Onypterygia longispinis Bates" (Drawer 361/5/2, BMNH).

Type Locality

Here restricted to Cerro Zunil, Quetzaltenango, Guatemala.

Diagnostic Combination

With character states of the *O. angustata* species group, restricted as follows. Elytra with marked aeneous cast, pronotum with both pairs of marginal setae, and elytral apices markedly acuminate (Fig. 10).

Description

With diagnostic combination of *O. longispinis* and the following.

Measurements and Proportions.—(Topotype female) TL intermediate (10.4 mm), WP/WH intermediate (1.49), LP/WP low (0.90), WP/WPb intermediate (1.26), LE/WE intermediate (1.77).

Prothorax.—Pronotum. Posterolateral impressions impunctate, or sparsely, shallowly punctate.

Pterothorax.—Mesepisternum partially punctate.

Elytra.—Elytron (Fig. 10), lateral margin narrowly rounded, not sinuate. Sutural apex rounded, or angulate. Interneurs 2–6 punctate for part of length. Discal setigerous punctures not foveate.

Legs.—Tarsomeres 1–3 of mid- and hind tarsi sulcate. Fore tarsomere 4, inner lobe longer than basal portion; hind tarsomere 4, outer lobe shorter than basal portion.

Male Genitalia.—(Fig. 56A–C) Internal sac, armature one spinose sclerite.

Variation

Specimens from Panzós, Sinanja, and Sabo have proportionately longer elytral spines and tend to be more purplish than those from Cerro Zunil and Tacaná.

Habitat

This species inhabits vegetation in montane tropical and humid to dry oak–pine forests, between 1300 and 1900 m altitude.

Geographical Distribution

This species is known from Guatemala and adjacent parts of Chiapas, in Mexico (Fig. 62).

Chorological Affinities

The range of *O. longispinis* is overlapped by the range of *O. angustata*, also of the *O. angustata* species group, and by the ranges of various species of the *O. famini*, *pusilla*, and *fulgens* groups. Additional details are provided below, under "Ecological Aspects."

Material Examined

We have seen about 75 specimens of *O. longispinis* from the following localities in Mexico and Guatemala.

MEXICO. Chiapas: Chincultic (Ruinas) on road to Montebello: 1 male, VIII.29.1982, Clark & Cave (AUEM); 1 female, VI.12.1989, H. F. Howden (UASM). Lagunas (or Lagos) de Montebello: 1 male, M. J. & C. A. Tauber (CUIC); 1 male, Cinco Lagos, 1500 m, oak–pine–Liquidambar forest, ix.21.1991, R. S. Anderson (CMNC); 3 males, 1 female, Laguna Pojoj, VI.12.1989, H. F. Howden (UASM); 1 male, Laguna Pojoj, 1500 m, VI.2.1990, H. & A. Howden (UASM); 1 female, Sumidero de Río Comitán, 1372 m, VIII.31.1974, D. E. & J. A. Breedlove (CASC); 1 male, Municipio Tenejapa,

Paraje Kulaktik, 1524 m, X.9.1981, D. E. Breedlove, C. G. Whitfield (CASC); Volcán Tacaná, 1524 m, bromeliads, XII.21 (UASM). **GUATEMALA. Alta Verapaz:** Panzós (MCZC). **Baja Verapaz:** 1 male, 5.2 km W Chilascó, 1650 m, oak–pine forest, V.24.1991, R. S. Anderson (CMNC); 3 females, 9.6 km W Chilascó, 1560 m, humid oak–pine forest, U–V light, 91–21, V.30.1991, D. Shpeley, G. E. & K. E. Ball (UASM); 1 female, same, 91–21, V.24.1991 (UASM); 1 female, 5.5 km W Cobán rd., from Pantin Jct., 1620 m, dry oak forest, beating vegetation, 91–17, V.31.1991, D. Shpeley, G. E. & K. E. Ball (UASM); 2 males, 1 female, Pantin Rd., 3 km S Cobán Hwy, 1600 m, VI.6.1993, H. & A. Howden (UASM); 1 male, 6–9 km E Purulhá, IV.15–16.1990, J. E. Wappes (JEWG); 3 males, 8 km S Purulhá, 1660 m, tropical montane forest, UV light, 91–05, V.19.1991, Shpeley, Ball & Ball (UASM); 2 males, 1 female, same, V.20.1991 (UASM); 1 male, 7 km NE Purulhá, 1500 m, VI.5.1993, H. & A. Howden (UASM); 2 males, 1 female, 14.5 km S Purulhá, 1600 m, tropical montane forest, beating vegetation, 91–13, V.21.1991, Shpeley, Ball & Ball (UASM); Sabo (BMNH, MCZC, USNM); 1 male, 1 female, 17.5 km N. Salamá (on #5), 1650 m, oak–pine forest, 93–38, VII.3.1993, R. S. Anderson (CMNC); 1 male, 19–24 km N. Salamá, 1372 m, V.25–31.1989, J. E. Wappes (JEWG). Sinanja (BMNH). **Quetzaltenango:** Cerro Zunil (BMNH, MCZC, USNM). **Zacapa:** 4 males, 2 females, Sierra de las Minas, 20.3 km N. Tecolutan, 1800–1900 m, tropical montane forest, beating, 91–34, VI.8.1991, Shpeley, Ball & Ball (UASM); 1 male, nr. San Lorenzo, 1219–1829 m, IV.13.1990, J. E. Wappes (JEWG).

Onypterygia angustata Chevrolat
(Fig. 53, 55, 57A–C, 60, 62)

Onypterygia angustata Chevrolat, 1835:160. Lectotype (here designated), male with posterior end of abdomen damaged by dermestid, labelled: “Chevrolat Carabidae. Fr. V. d. Poll. Pres. 1909, E. B. Poulton.”; “TYPE COL: 149 *Onypterygia angustata* Chevr. HOPE DEPT. OXFORD” (OXUM).—Bates, 1882: 132 (in part).

Onychopterygia angustata; Gemminger and Harold, 1868:384 (invalid emendation). Chaudoir, 1878: 276.

Type Locality

Cruz Blanca, Veracruz, Mexico.

Diagnostic Combination

With character states of *O. angustata* species group, restricted as follows. Pronotum with two pairs of lateral setae, posterolateral angles of pronotum not sparsely punctate, elytron with apex in form of an obtuse angle, and interneurs finely but distinctly punctate. In Mexico, *O. angustata* and *O. pseudangustata* are the only small (length less than 12 mm) species in the genus with a denticulate elytral apex. In the vicinity of Jalapa, Veracruz, where these species are sympatric, *O. angustata* differs by having both pairs of lateral marginal setae and distinctly punctulate elytral interneurs; also, most individuals are smaller, with the pronotum more narrowed basally, and the elytra coppery rather than green. In Costa Rica, the elytral apices of *O. angustata* tend to be only slightly angulate.

Description

With diagnostic combination of *O. angustata* and the following.

Measurements and Proportions.—(Male, Jalapa, Veracruz) TL small (7.9 mm), WP/WH intermediate (1.33), LP/WP low (1.00), WP/WPb low (1.18), LE/WE intermediate (1.74).

Color.—Antennae with basal and apical antennomeres piceous to black, or rufopiceous. Palpi piceous. Elytra with disc bronze-green, metallic. Femora, tibiae, and tarsi piceous to black, or rufopiceous.

Chaetotaxy.—Pronotum, lateral setae two pairs.

Prothorax.—Pronotum (Fig. 53). Posterolateral impressions sparsely punctate.

Pterothorax.—Mesepisternum partially punctate.

Elytra.—Elytron, lateral margin narrowly rounded, not sinuate. Apex acuminate, spine shorter; sutural apex rounded. Interneurs 2–6 impunctate. Discal setigerous punctures not foveate.

Hind Wings.—Venation as in Figure 55.

Legs.—Tarsomeres 1–3 of middle and hind tarsi sulcate. Fore tarsomere 4, inner lobe as long as basal portion; hind tarsomere 4, outer lobe as long as basal portion.

Male Genitalia.—(Fig. 57A–C). Internal sac, armature two spinose sclerites.

Ovipositor.—Left stylomeres 1 and 2 as in Figure 60.

Habitat

Adults were collected in montane tropical, and mesic oak–pine forests, between 1000 and 2300 m altitude. Many specimens were taken from bromeliads, most others by beating vegetation.

Geographical Distribution

The known range of *O. angustata* extends from Panama northward to central Veracruz, in eastern Mexico (Fig. 62).

Chorological Affinities

This species is sympatric, at least in part, with *O. famini*, *O. pusilla*, *O. longispinis*, *O. fulgens*, *O. tricolor*, and *O. hoepfneri*.

Material Examined

We have seen 222 specimens of *O. angustata* from the following localities. Some were intercepted at U. S. ports of entry with various plants, including orchids, from Guatemala, Honduras, Mexico, and Nicaragua.

MEXICO. Chiapas: 2 females, Chincultic, VIII.29.1982, Clark & Cave (AUEM); 1 male, El Sumidero, 1000 m, X.21.1988, R. Turnbow (RHTC); 1 female, same, V.25.1990, H. & A. Howden (UASM); 48 & 54 km N. Huixtla (UASM); Pueblo Nuevo, 5 & 35 km S Pueblo Nuevo (UASM); 2 females, 14.3 km S Tapilula, 1463 m, cloud forest, VII.7.1983, R. S. Anderson, W. Maddison (UASM); 1 male, 1 female, Volcán Tacaná, Union Juárez, NE slope Barranca Providencia, 1600 m, montane tropical forest, *ex* vegetation overhanging road cut, XII.24–25.1975, H. E. Frania and J. Belicek (UASM); 16 males, 9 females, Volcán Tacaná, 1524 m, *ex* bromeliads, XII.21.1976, H. E. Frania, D. L. C. Proctor (UASM). **Colima:** 1 male, 14 km E Minatitlán, VII.17.1990, J. E. Wappes (JEWEC). **Distrito Federal:** 1 specimen, from Mexico City, intercepted with orchids (USNM). **Hidalgo:** 2 females, Rte. 105, 7.7 km S Tlanchinol, VII.20.1988, R. Turnbow (RHTC). **Jalisco:** 1 specimen, Sebastián, Sierra Madeiro Mts., 1800 m, II.1 (CASC). **Michoacán:** 1 female, Tingambato, XI.20.1980, H. Brailovsky (CASC). **Oaxaca:** Juquila (BMNH); Juquila Mixes, V.1971, M. S. Miller (CNCI); 3 specimens, 55.5 km N. Pochutla, III.19–20.1966, Ball and Whitehead (UASM); 2 specimens, 30.7 km S Suchixtepec, in bromeliads, III.17.1966, Ball and Whitehead (UASM). **Puebla:** 1 female, Xicotepec de Juárez, VII.13.1980, H. Brailovsky (CASC). **Veracruz:** Córdoba (BMNH); 5 males, 3 females, 3.9 km NE Coscomatepec, 1310 m, in bromeliads on acacias, 78B-26, XI.19.1978, G. E. & K. E. Ball (UASM); 11.6 km NE Coscomatepec, bromeliads (UASM); 1 male, Hwy. 140, 7.1 km N. Huatusco, 1300 m, beating weeds & vines, VIII.15.1987, J. K. Liebherr, D. A. Millman (CUIC); 20 specimens, 16.7 km SW Huatusco, 1433 m, in bromeliads, III.8.1966, Ball and Whitehead (UASM); 1 male, Jalapa, Instituto de Ecología, 1300 m, *ex* epiphytes, XI.25.1994, Purrington & C. Drake (FFPC); 1 female, Jalapa, La Pitahaya, 1300 m, *ex* epiphytes, XII.1.1994, Purrington & C. Drake (FFPC); 1 male, 3 km S Jalapa, 1350 m, V.25–30.1991, B. Ratcliffe, J. Ashe, M. Jameson (SEMC); 1 female, 1 km N. Jilotepec, beating, 1300 m, VII.31.1990, J. K. Liebherr (CUIC). 1 specimen, Metlac, in bromeliads, XII (FSCA). **BELIZE. Toledo:** Sarstoon River (BMNH). **COSTA RICA. Cartago:** 2 specimens, Cervantes, 1450 m, IV.8 (USNM); 5 specimens, Tres Ríos (MCZC). **Puntarenas:** 5 specimens, Coronado, on blossom “plomillo,” V.23 (USNM); 1 female, Monteverde, 1372 m, V.21–26.1979, J. M. & B. A. Campbell (CNCI); 1 male, same, 1500 m, II.26.1991, K. M. Hamilton (UASM); 1 male, same, H. & A. Howden (UASM). **San José:** 2 specimens, San José, II.3, XI.2 (USNM). **EL SALVADOR.** 1 female, Cerro Verde, V.1.1971, H. F. Howden (UASM). **La Libertad:** 2 specimens, Volcan El Boquerón (Nègre Coll., MNHP). **Santa Ana:** 1 specimen, Hidalgo Montecristo, Metapán, 2300 m, cloud forest (FSCA). **GUATEMALA. Baja Verapaz:** 1 male, 8.6 km W Chilascó, 1560 m, VI.7.1993, U-V light, H. & A. Howden (UASM). **Chimaltenango:** 2 specimens, S. P. Yepocapa, 1463 m, sweeping, V.10, light, V.12 (FMNH); 1 specimen, same (USNM). **El Progreso:** 5 males, 6 females, 20 km N. Estacion de la Virgen, 1900 m, cloud forest, VI.8.1991, R. S. Anderson (CMNC); 1 male, 21 km N. Estacion de la Virgen, 1829 m, VI.3.1991, J. E. Wappes (JEWEC). **Escuintla:** 1 male, 4 km N. Palín, VI.21.1966, J. M. Campbell (CNCI). **Guatemala:** 3 males, Guatemala City, 1 km SE La Puéblito, 1700 m, oak scrub forest, VI.11.1991, R. S. Anderson (CMNC); 1 male, 4 females, same, 1850 m, oak–pine forest, beating vegetation, 91-37, VI.10.1991, Shpeley, Ball & Ball (UASM); 2 males, 5 females, Guatemala City, Universidad del Valle campus, 1511 m, oak–pine forest, 91-36, VI.10.1991, Shpeley, Ball & Ball (UASM); 15 males, 9 females, Puente Parada, 14.5 km SE Guatemala City, 1790

m, oak–pine forest, beating vegetation, 91–41, VI.13.1991, Shpeley, Ball & Ball (UASM); 2 females, same, A. Howden (UASM). **Jalapa:** 1 female, Mataquescuintla, Finca Concepción, VII.2.1986, J. M. Campbell (CNCI). **Sacatepéquez:** Capetillo (BMNH); 1 male, 4.5 km NW San Miguel Dueñas, 1760 m, VI.12.1991, H. & A. Howden (UASM). **Zacapa:** 2 females, 19 km N. Estacion del Virgen, 1219 m, IV.18–21, 1990, J. E. Wappes (JEWG); 1 female, Sierra de las Minas, San Lorenzo, 1740 m, VII.18.1986, J. M. Campbell (CNCI); 7 males, 7 females, Sierra del Espíritu Santo, 3 km SE La Union, 1400–1500 m, U–V light, 91–31, VI.6.1991, Shpeley, Ball & Ball (UASM). **HONDURAS.** **Federico Morazán:** 1 female, 37 km E Tegucigalpa, VIII.8.1982 (TAMU); 2 females, Cerro Uyuca, 30 km E Tegucigalpa, 1800 m, V.16.1994, H. & A. Howden (UASM); 2 males, 2 females, V.19.1994 (UASM); 1 female, V.30.1994 (UASM); 1 specimen, near Tegucigalpa, intercepted with plants, II (FSCA); 1 male, 1 female, 6 km SE Zamorano, 850 m, U–V light, H. & A. Howden (UASM). **Intibuca:** 1 female, 6 km W La Esperanza, XII.3.1995, R. H. Turnbow (RHTC). **Olancho:** 5 males, 12 females, Parque Nacional La Murala, at MV + UV light, V.24–VI.12.1995, R. H. Turnbow (RHTC); 1 male, 2 females, same locality, XI.29.1995, R. H. Turnbow (RHTC). **Paraíso:** 1 male, 4 females, Cerro Montserrat, 7 km SW Yuscarán, 1800 m, V.21.1994, H. & A. Howden (UASM); 1 male, 4–7 km SE Danli, XI.29.1995, R. H. Turnbow (RHTC). **NICARAGUA.** 1 male, 20 km N. Matagalpa, VII.1989, F. Reinholdt (UNAN); 1 specimen, “Nicaragua,” intercepted with plants XI (FSCA). **PANAMA.** **Chiriquí:** 1 male, 1 female, Bambito, S. Cerro Punta, 1585 m, IV.23.1976, M. S. Carter & C. L. Mollineux (CASC); 1 female, 3 km W Cerro Punta, 8°51'N, 82°36'W, 1720 m, XI.26.1976, H. P. Stockwell (UASM); Volcán de Chiriquí (BMNH).

Onypterygia pseudangustata, new species

(Fig. 54A; 58A, B; 59A, B; 61, 62)

Bates, 1882:132 (as *O. angustata* Chevrolat).

Type Material

Fifteen specimens, labelled as follows. Holotype male, labelled: “6 mi. East/Teziutlan, Pueb MEX./VII.4–6,60/H. F. Howden” (CNCI). Allotype female, labelled: “Jalapa/Mexico/Hoege” (BMNH). Thirteen paratypes, as follows. Male, labelled same as holotype. Nine, labelled same as allotype. Male and female, labelled: “Jalapa/Mexico/Hoege”; “Ex/Godman/and/Salvin” (MCZC). Male, labelled: “5 mi. N./Teziutlan, Pue./27.VI.1975 MEX.”; “J. E. Gillasp/Collector” (CUIC).

Type Material

Bates (1882:132) included the Hoege specimens noted above in his series of *O. angustata*.

Type Locality

9.7 km east of Teziutlán, Puebla, Mexico.

Specific Epithet

Two words, Greek, *pseudo-*, meaning false, and Latin, *angustata*, the name of another species of *Onypterygia*. Together, they mean “false-angustata,” in allusion to the similarity and sympatry of, and past confusion with, *O. angustata*.

Diagnostic Combination

With character states of *O. angustata* species group, restricted as follows. Pronotum with a single pair (posterolateral) of lateral setae and elytral apex angulate, but not acuminate. Compared to adults of *O. angustata*, those of *O. pseudangustata* are larger on average, with the pronotum less narrowed posteriorly, the elytra green rather than coppery, the preapical lateral elytral calli more prominent, and the elytral interneurs deeper and much less distinctly punctulate.

Description

With diagnostic combination of *O. pseudangustata*, and the following.

Measurements and Proportions of Holotype.—TL small (9.0 mm), WP/WH intermediate (1.56), LP/WP low (0.84), WP/WPb intermediate (1.25), LE/WE intermediate (1.73).

Color.—Antennae with basal and apical antennomeres piceous to black. Palpi piceous. Elytra with disc metallic green. Femora, tibiae, and tarsi piceous to black.

Prothorax.—Pronotum (Fig. 54A). Posterolateral impressions densely punctate.

Pterothorax.—Mesepisternum impunctate.

Elytra.—Elytron, humerus broadly rounded; lateral margin slightly sinuate medially. Sutural apex rounded. Interneurs 2–6 punctate for part of length. Discal setigerous punctures foveate.

Legs.—Tarsomeres 1–2 of mid- and hind tarsi sulcate. Fore tarsomere 4, inner lobe as long as basal portion; hind tarsomere 4, outer lobe as long as basal portion.

Male Genitalia.—(Fig. 58A, B; 59A, B) Internal sac (Fig. 59B), armature two spinose sclerites on right side.

Geographical Distribution

This species is known only from a small area in the eastern part of the Transvolcanic Sierra of central Mexico (Fig. 62).

Chorological Affinities

The range of *O. pseudangustata* is overlapped by that of *O. angustata*, and probably by that of wide-ranging species in the *O. famini* and *O. fulgens* species groups, and *O. batesi* in the *O. aeneipennis* group. It is allopatric in relation to the range of its closest relative, *O. sriblingi*, n. sp.

Phylogenetic Relationships

This species is the postulated adelphotaxon of *O. sriblingi*, n. sp.

Material Examined

We have seen the type series of *O. pseudangustata* only; for details see above.

Onypterygia sriblingi, new species (Fig. 54B, C; 62)

Type Material

Four specimens, as follows. Holotype male, labelled: "MEX.OAXACA/Vista Hermosa/04 Jul 1982/M. A. Ivie colr." (CUIC). Allotype female, labelled same as holotype (CUIC). Paratypes, two males, one labelled same as holotype; one labelled "MEXICO: Oaxaca/Vista Hermosa/beating, 3-VII-1982/J. B. Stribling, colr." (CUIC).

Type Locality

Vista Hermosa, Oaxaca is 4.8 km south of Valle Nacional, on Highway 175 (ca. 17°45'N, 96°21'W), at an altitude of 610 m. This locality is near the type locality of *O. exeuros*, n. sp.

Specific Epithet

This is based on the Latinized genitive form of the surname of J. B. Stribling, one of the collectors of the type series, and a specialist on Ptilodactylidae and related byrrhoid families.

Diagnostic Combination

With character states of the *O. angustata* species group, restricted as follows. Recognized easily by the pronotum with a single pair of lateral setae, and acuminate elytral apices. The latter feature is similar to that of *O. kathleenae*, n. sp., and *O. longispinis* Bates. However, these species are distinguished readily by the features noted in the key.

Description

With diagnostic combination of *O. sriblingi* and the following.

Measurements and Proportions of Holotype.—TL small (8.32 mm), WP/WH intermediate (1.38), LP/WP low (0.86), WP/WPb intermediate (1.12), LE/WE intermediate (1.67).

Color.—Antennae with basal and apical antennomeres piceous to black. Palpi piceous. Elytra bright coppery. Femora, tibiae, and tarsi piceous to black.

Prothorax.—Pronotum (Fig. 54B). Posterolateral impressions densely punctate; angles obtuse.

Pterothorax.—Mesepisternum partially punctate.

Elytra.—(Fig. 54C) Elytron, lateral margin slightly sinuate medially. Apex spinose, shorter; sutural apex rounded. Interneurs 2–6 punctate for part of length. Discal setigerous punctures foveate.

Legs.—Tarsomeres 1–2 of mid- and hind tarsi sulcate. Fore tarsomere 4, inner lobe as long as basal portion; hind tarsomere 4, outer lobe as long as basal portion.

Male Genitalia.—Internal sac with two spinose sclerites, both on right side, one basal and one nearly at apex.

Habitat

On vegetation, probably in low montane rain forest.

Geographical Distribution

This species is known from the type locality only (Fig. 62).

Chorological Affinities

This species is isolated geographically from the ranges of the other species of the *angustata* group. However, its range is overlapped by the ranges of the *famini*, *aeneipennis*, *pusilla*, and *fulgens* species groups.

Phylogenetic Relationships

This species is the postulated adelphotaxon of *O. pseudangustata*, based on general similarity and the shared position of the spinose sclerites of the internal sac of the male genitalia.

Material Examined

We have seen the type series of *O. striblingi* only; for details see above.

The *fulgens* Species Group

Recognition

Because of marked interspecific variation, this group is not characterized simply. Included are all species exhibiting a combination of pronotum with lateral margins not or only slightly sinuate posteriorly, and each elytron with a distinct preapical lateral callus, and/or interneur 1 deeper preapically than interneur 2. Further, this group contains all members of the genus with elytra bicolored transversely or with alternating stripes, those with sharply bidentate elytral apices, or combination of fewer than two pairs of lateral pronotal setae and indistinct posterolateral angles.

Description

With character states of *Onypterygia*, restricted as follows. Body small to large in size, elytra elongate, measurements and proportions as in Table 2.

Color.—Ventral surface of body and appendages (except elytra) black to piceous; dorsal surfaces of head, pronotum, and elytra variously black to piceous, aeneous, green, cupreous, or maroon, or various combinations of these, including alternate striping of elytra with cupreous and green, or fasciae of maroon and dark blue.

Microsculpture.—Head smooth, without microlines, or microlines distinct, mesh pattern isodiametric. Pronotum smooth, without microlines, or microlines distinct, mesh pattern transverse. Elytra with surface smooth, without microlines, or microlines distinct, mesh pattern isodiametric to transverse, sculpticells flat to slightly convex.

Luster.—Dorsal surface shining, or at least elytra dull.

Chaetotaxy.—Pronotum without lateral setae, or with one or two pairs. Elytra, in or near interval 3, with two pairs of discal setae to plurisetose. Abdominal sterna IV–VI each with one or more pairs of ambulatory setae, sternum VII of males with one or two pairs of posterior marginal setae, females with two or more pairs.

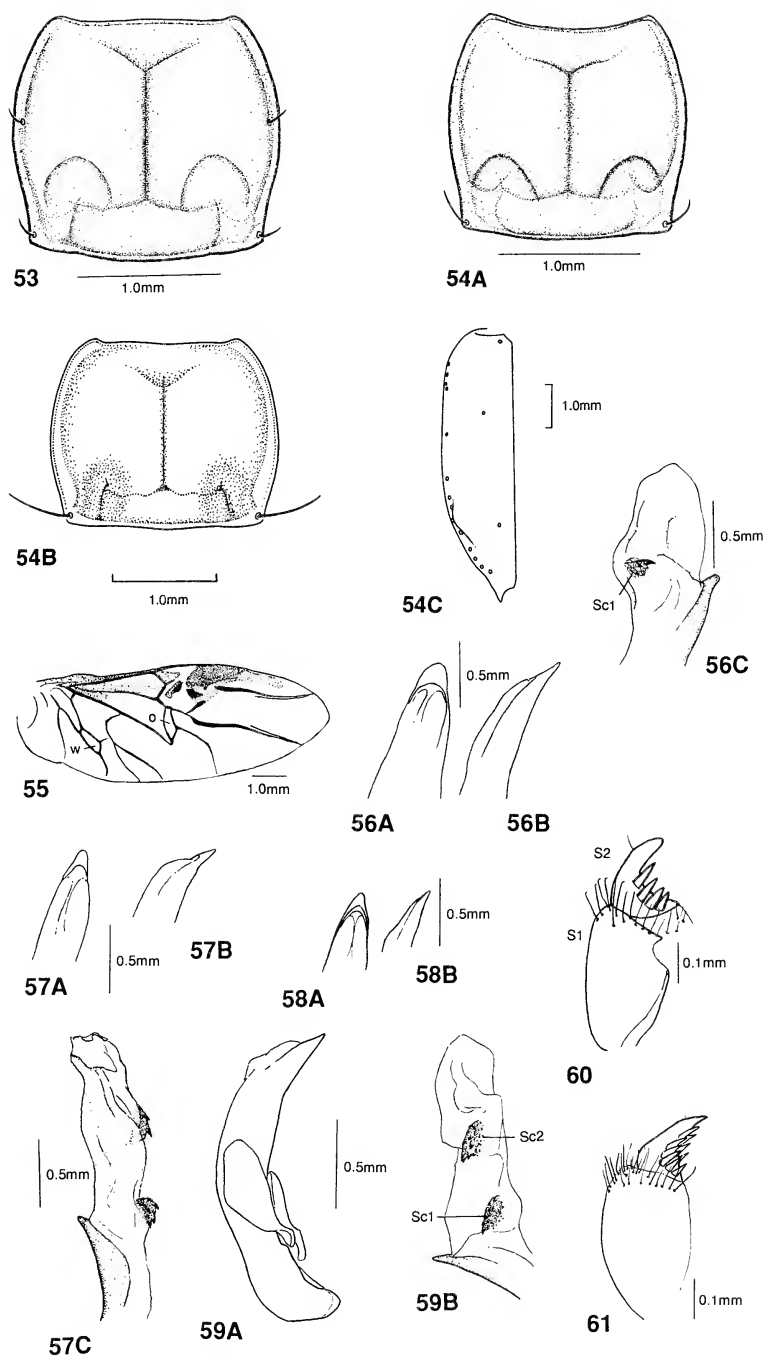


Fig. 53–61.—Line drawings of adult structural features of the *O. angustata* species group. Fig. 53–54A, B, pronotum, dorsal aspect of: 53, *O. angustata* Chevrolat; 54A, *O. pseudangustata*, n. sp.; 54B, *O. sriblingi*, n. sp. Fig. 54C, left elytron, dorsal aspect of *O. sriblingi*, n. sp. Fig. 55, left hind wing, ventral aspect, of *O. angustata* Chevrolat. Fig. 56–59, male genitalia of: 56, *O. longispinis* Bates: A, B, median lobe, apical portion, dorsal and left lateral aspects, respectively; C, median lobe, left lateral

Head.—Frons and vertex smooth, without supraorbital carina each side.

Prothorax.—Pronotum as in Figure 63–74. Surface smooth or shallowly and sparsely punctate posterolaterally; posterolateral angles obtuse or broadly rounded, lateral margins slightly or not sinuate, beaded partially or completely, or not beaded; posterior pair of setigerous punctures on beads, or in contact with lateral margins; lateral grooves moderately to markedly wide, especially posteriorly. Prosternum with intercoxal process rounded apically.

Pterothorax.—Metathorax normal, metepisternum distinctly longer than wide, or metathorax short, metepisternum nearly quadrate.

Elytra.—Elongate, humeri fully developed, discal and umbilical setigerous punctures foveate or not. Interneurs fine, shallowly impressed to obsolete; interneur 1 posteriorly on apical declivity more deeply impressed than interneur 2. Preapical lateral calli distinct. Apex acuminate or not; sutural apex angulate, acuminate, or rounded (cf. Fig. 7).

Hind Wings.—(Fig. 78, 79) Macropterous, membrane hyaline or infuscated, wedge cell short; or brachypterous.

Legs.—Tarsomeres 2–4 ventrally with climbing setae markedly dense (Fig. 11F, G:cs). Tarsomere 5 with ventrolateral setae normally developed (Fig. 11G:vs). Tarsal claws with pectinations more extensive (Fig. 11H).

Male Genitalia.—Median lobe (Fig. 80–100) with apical portion short (Fig. 81; 83A, B), narrowly triangular, to elongate (Fig. 89A, B), apex narrow or broadly rounded (Fig. 82A). Internal sac moderately to markedly elongate (Fig. 82C; 87; 88; 97A, B; 98–100), armed variously with spinose sclerites or setose spines.

Ovipositor.—Stylomere 2 (Fig. 15, 16, 101–106) slightly falcate, of two types: form 2, ensiform setae ca. 12, and concentrated on or near dorsoapical margin; or form 3, ensiform setae more numerous, in form of dense pad on lateral surface.

Habitat

Most species of this group are confined to tropical montane forests between 500 and 1500 m altitude, but some range to sea level in tropical deciduous forest, and to pine–fir forest at 2500 m altitude.

Geographical Distribution

The range of this species group extends throughout Middle America from northern Mexico to Panama, and into northern South America (Fig. 107–110).

Chorological Affinities

See “Chorological Affinities” for *famini* group, above.

Phylogenetic Relationships

The *fulgens* species group seems to be the most highly evolved in *Onypterygia*. It is postulated to be the adelphotaxon of the *angustata* group, based primarily on shared details of elytral structure.

Included Species

This group includes the following 14 species: *O. iris* Chaudoir; *O. championi* Bates; *O. donato* Ball and Shpeley; *O. chrysura* Bates; *O. kathleenae*, n. sp.; *O. exeuros*, n. sp.; *O. polytreta*, n. sp.; *O. crabilli*, n. sp.; *O. quadrispinosa* Bates;

aspect, with internal sac everted. 57, *O. angustata* Chevrolat: A, B, median lobe, apical portion, dorsal and left lateral aspects, respectively; C, median lobe, apical portion, right lateral aspect, with internal sac everted. 58, *O. pseudangustata*, n. sp. (6 mi. e. Teziutlan, Puebla, Mex.): A, B, median lobe, dorsal and left lateral aspects, respectively. 59, *O. pseudangustata*, (Jalapa, Veracruz, Mex.): A, median lobe and parameres, left lateral aspect; B, median lobe, apical portion, right lateral aspect, with internal sac everted. Fig. 60, 61, ovipositor, left stylomeres 1 and 2, of: 60, *O. angustata* Chevrolat; 61, *O. pseudangustata*. Legend: o—oblongum cell; S1, S2—stylomeres 1 and 2, respectively; Sc1, Sc2—spinose sclerites 1 and 2, respectively; w—wedge cell.

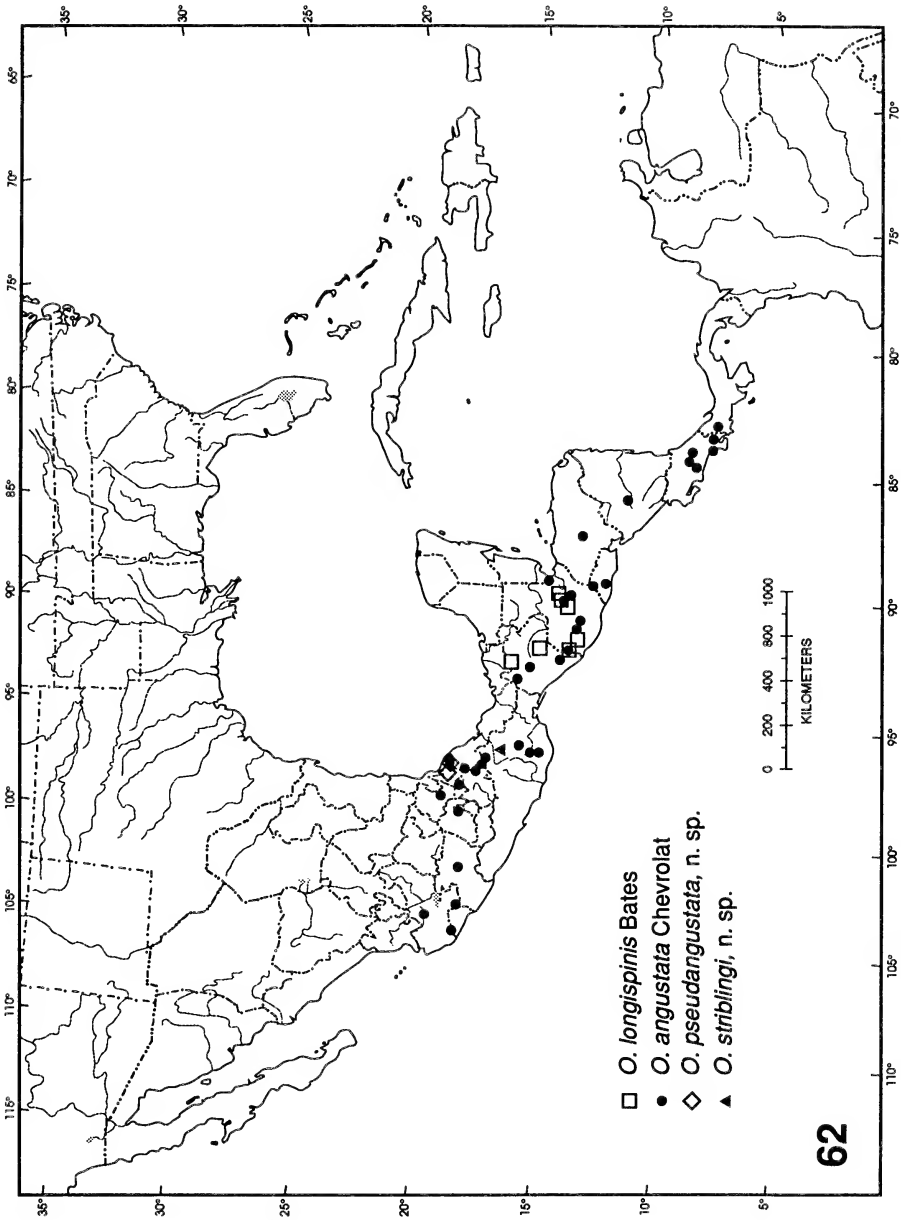


Fig. 62.—Map of southern North America, Middle, and northern South America, showing positions of collecting records for the *O. angustata* species group.

O. scintillans, n. sp.; *O. fulgens* Dejean; *O. tricolor* Dejean; *O. hoepfneri* Dejean; and *O. sallei* Chaudoir.

Onypterygia iris Chaudoir
(Fig. 63; 75; 80A–C; 101; 107)

Onypterygia iris Chaudoir, 1863:225. Lectotype (here designated), male, labelled: "Iris (Sallé)"; "Ex Musaeo A. Sallé 1897"; (Oberthür–Chaudoir Collection, MNHP). Bates, 1882:130.

Onychopterygia iris; Gemminger and Harold, 1868:384 (invalid emendation). Chaudoir, 1878:275.

Type Locality

Córdoba, Veracruz, Mexico. In the original description, Chaudoir (1863:225) records for this species only a single locality: Córdoba, state of Veracruz.

Diagnostic Combination

With character states of the *fulgens* species group, restricted as follows. The most obvious feature of *O. iris* adults is the longitudinally striped elytra, which is shared with adults of *O. championi*, *O. polytreta*, and *O. donato*. The long metepisternum separates *O. iris* from *O. donato* (metepisternum short, brachypterous). The elytra with nonfoveate discal punctures and simple apices distinguish adults of *O. iris* from those of *O. championi* and *O. polytreta*. Form of median lobe, and internal sac of males and stylomere 2 of females are unique within the genus.

Description

With diagnostic combination of *O. iris* and following.

Measurements and Proportions.—TL large (11.0 mm), WP/WH low (1.38), LP/WP intermediate (0.76), WP/WPb intermediate (1.24), LE/WE intermediate (1.75).

Color.—Head piceous-black. Basal antennomeres black, nonmetallic. Elytra with discal pattern bi-colored-striped; coppery and green. Femora, tibiae, and tarsi piceous to black.

Microsculpture, Mesh Pattern.—Head, microlines partially effaced, isodiametric; pronotum, transverse; elytra, isodiametric.

Chaetotaxy.—Pronotum, lateral setae two pairs; elytron, discal setae three; dorsoapical portion of hind femur without setae; abdominal sterna IV–VI one pair of setae each; abdominal sternum VII, marginal setae male, one pair; female, more than two pairs.

Head.—Genae smooth, not rugose. Eyes flattened slightly.

Prothorax.—Pronotum (Fig. 63). Anterior bead complete; lateral beads absent. Posterolateral impressions impunctate, or sparsely punctate; angles broadly rounded. Lateral margins sinuate beaded narrowly, bead indistinct anteriorly.

Pterothorax.—Mesepisternum partially punctate. Metepisternum elongate.

Elytra.—(Fig. 75) Surface smooth. Elytron, humerus broadly rounded; lateral margin slightly sinuate medially. Apex rounded; sutural apex rounded. Interneurs 2–6 continuous, shallow, impunctate. Discal and umbilical setigerous punctures foveate.

Hind Wings.—Macropterous.

Legs.—Tarsomere 1 of middle and hind tarsi sulcate. Fore tarsomere 4, inner lobe longer than basal portion; hind tarsomere 4, outer lobe as long as basal portion.

Male Genitalia.—Median lobe in dorsal aspect (Fig. 80A) with apical portion moderately elongate, narrow, twisted; apex in left lateral aspect (Fig. 80B) very narrowly rounded, essentially acute. Internal sac (Fig. 80C), relatively short; basal lobes two; preapical lobes absent; armature absent.

Ovipositor.—(Fig. 101) Stylomere 2 form 1, ensiform setae marginal.

Habitat

This species lives in wet tropical montane forest, between altitudes of 800 and 1650 m. Some adults were found on the ground, but the species is probably arboreal.

Geographical Distribution

The known range of this species is confined to Chiapas and central Veracruz, around Jalapa, Orizaba, and Córdoba (Fig. 107). The record from "Guanajuato" is questionable.

Chorological Affinities

The range of this species is separated from that of its closest relatives, the Panamanian *O. championi* Bates and the Costa Rican *O. donato* Ball and Shpeley, but is overlapped by other species of the *O. fulgens* group, and by various species of most other groups of *Onypterygia*.

Phylogenetic Relationships

Ball and Shpeley (1992:407) postulated that *O. iris* is the adelphotaxon of *O. donato* + *O. championi*.

Material Examined

We have seen 25 specimens of *O. iris*, in addition to records cited by Bates (1882), as follows. All specimens are from localities in Mexico.

Chiapas: 1 male, Chiapas–Oaxaca border, 21 km W Rizo de Oro, along ridge SE Cerro Baul, 1615 m, cloud forest, IX.6.1972, C. Mollineux (CASC); 1 male, 8.6 km S Rayon, IX.12.1981, Clark & Coe (AUEM). **Guanajuato:** Guanajuato, E. Duges (Nègre Coll., MNHP; locality requires confirmation). **Veracruz:** 1 male, 1 female, Actopan, IX.18.1982, H. Brailovsky (CASC); 1 female, Coatepec, VII.25.1955, P. & C. Vaurie (AMNH); Fortín de las Flores (CSIC, FSCA, UASM); 1 specimen, 5.5 km E Huatusco, cloud forest, 1036 m, VI.21.1966, Ball and Whitehead (UASM); 1 male, Hwy. 140, 1 km N. Huatusco, 1200 m, on logs at night, VIII.14.1987, J. K. Liebherr, D. A. Millman (CUIC); 1 male, Jalapa (MCZC); 1 female, Jalapa, Instituto de Ecología, 1300 m, spider midden, XI.21.1994, Purrington & C. Drake (FFPC); 1 female, 3 km S Jalapa, 1350 m, V.25–30.1991, B. Ratcliffe, J. Ashe, M. Jameson (SEMC); 1 specimen, 3.2 km NE Jilotepec, IX.26 (TAMU); 1 male, Las Minas, 1300 m, at light, VIII.18.1987, D. A. Millman (CUIC); Orizaba, "Sierra de Durango" (Nègre Coll., MNHP; locality probably in Veracruz; see Selander and Vaurie, 1962).

Onypterygia championi Bates

(Fig. 64, 76, 81, 107)

Onypterygia championi Bates, 1882:130. Lectotype male, labelled: "TYPE H. T." [circular, ringed with red]; "V. de Chiriquí/2–3000 ft./Champion"; "B.C.A. Col. I.1/ Onypterygia/ championi/ Bates"; "Onypterygia/ championi/ Bates" [handwritten]; "LECTO-/TYPE" [circular, ringed with purple]; "♂ BMNH/ LECTOTYPE/ det. D. R. Whitehead [red underline] Onypterygia/ championi/ Bates/ det. D. R. Whitehead"; (BMNH).

Type Material

Although the BMNH has only the single specimen noted above, and although the description records but a single measurement, Bates may have had more than a single specimen when he described *O. championi*. In the USNM, for example, is a single male, labelled "V. de Chiriquí/2–3000 ft./Champion"; H. W. Bates/ Biol. Cent. Amer."; "m.l. & sac/drawn/D. R. Whitehead"; "Onypterygia/ championi/Bates" [handwritten, in Bates' hand]. But it does not have the "B.C.A." label characteristic of Bates' type material. Possibly then, this specimen was seen by Bates subsequent to publication of the species description. Nonetheless, in view of the uncertainty, the type specimen in the BMNH is regarded as a lectotype.

Type Locality

Volcán de Chiriquí, Chiriquí, Panama.

Diagnostic Combination

With character states of the *O. fulgens* species group, restricted as follows. *Onypterygia championi* is the only species of *Onypterygia* with a combination of striped elytra, acuminate elytral apices, and foveate punctures in interval 3.

Description

With diagnostic combination of *O. championi*, and the following.

Measurements and Proportions.—TL large (11.3 mm), WP/WH low (1.55), LP/WP low (0.78), WP/WPb intermediate (1.30), LE/WE intermediate (1.75).

Color.—Head dark green. Basal antennomeres partially metallic green. Pronotum dark green. Elytra with discal pattern bicolored-striped coppery and green.

Chaetotaxy.—Pronotum, lateral setae two pairs; elytron, discal setae three; dorsoapical portion of hind femur without setae; abdominal sterna IV–VI one pair of setae each; abdominal sternum VII, marginal setae male, one pair; female, two pairs.

Head.—Genae smooth, not rugose. Eyes flattened slightly.

Prothorax.—Pronotum (Fig. 64). Anterior bead complete; lateral beads absent for most of length. Posterolateral impressions impunctate, or sparsely punctate; angles broadly rounded. Lateral margins not sinuate, beaded narrowly.

Pterothorax.—Mesepisternum impunctate. Metepisternum elongate.

Elytra.—Surface smooth. Elytron (Fig. 76), humerus broadly rounded; elytron, lateral margin slightly sinuate medially. Apex acuminate, shorter; sutural apex rounded. Interneurs 2–6 continuous, shallow, completely punctate. Discal and umbilical setigerous punctures foveate.

Hind Wings.—Macropterous.

Legs.—Tarsomeres 1–3 of middle and hind tarsi sulcate. Fore tarsomere 4, inner lobe longer than basal portion; hind tarsomere 4, outer lobe as long as basal portion.

Male Genitalia.—(Fig. 81) Median lobe in left lateral aspect with apical portion short, triangular in outline, apex acute. Internal sac moderately elongate; basal lobes and preapical lobes absent; armature two mediopreapical spinose sclerites, left laterally.

Ovipositor.—Stylomere 2 form 2.

Habitat

Specimens of *O. championi* have been collected in wet montane tropical forest.

Geographical Distribution

This species is known only from the mountains of Costa Rica and Panama (Fig. 107).

Chorological Affinities

This species is allopatric in relation to the range of its postulated adelphotaxon, the Costa Rican *O. donato*. The range of *O. championi* is overlapped only by the ranges of *O. angustata* (*angustata* group) and *O. tricolor* (*fulgens* group).

Phylogenetic Relationships

See this topic for *O. iris*, above.

Material Examined

In addition to the holotype and the male referred to above, we have seen ten specimens of *O. championi* from the following localities.

COSTA RICA. Puntarenas: Parque Nacional Amistad, Finca Cafrosa, Est. Mellizas, 1300 m, V.1990, L-S 316100-596100, M. Ramirez & G. Mora (INBC) 1 male, INBIO CR 1000-264710; 1 male, INBIO CR 1000-264711; 3 males, 316100, 599200; same locality, except VI.19–VII.26, 1990, R. Delgado (INBC) 1 male, INBIO CR 1000-667789; 1 male, Est. Biol. Las Alturas, 1500 m, III.23–V.2.1992, L-S-322500, 591300, Coto Brus, F. Araya (INBC). **PANAMA. Chiriquí:** 1 female, Las Lagunas, V.13.1981, J. E. Wappes (JEW); 1 male, 15 km E Río Sereno, V.23–25.1982, E. Giesbert (CASC); 1 female, 2 km N. Sta. Clara, Hartmann's Finca, 8°51'N, 82°36'W, 1300 m, V.24–25.1977, H. & A. Howden (UASM); 1 male, 1 female, same locality, 1450 m, wet montane tropical forest, VI.15.1995, R. S. Anderson (CMNC); 1 male, 1 female, N. Santa Clara, 8°51'N, 82°46'W, v.31.1977, H. P. Stockwell (UASM).

Onypterygia donato Ball and Shpeley
(Fig. 107)

Onypterygia donato Ball and Shpeley, 1992:403. Holotype female (for details of labelling, see original description).

Type Locality

La Amistad National Park, Puntarenas, Costa Rica.

Diagnostic Combination

With character states of *O. fulgens* species group, restricted as follows. Features are the same as for *O. championi* Bates (see above) plus a reduced metathorax (metepisternum relatively short).

Description

With diagnostic combination of *O. donato* and the following.

Habitus.—As in Ball and Shpeley, 1992:405, fig. 1.

Measurements and Proportions of Holotype.—TL small (8.1 mm), WP/WH low (1.67), LP/WP low (0.80), WP/WPb intermediate (1.20), LE/WE intermediate (1.50).

Color.—Head and pronotum dark green. Basal antennomeres black, nonmetallic. Elytra with discal pattern bicolored-striped coppery and green.

Microsculpture, Mesh Pattern.—Head, isodiametric; pronotum, transverse; elytra, isodiametric.

Chaetotaxy.—Pronotum, lateral setae two pairs; elytron, discal setae two; dorsoapical portion of hind femur without setae; abdominal sterna IV–VI one pair of setae each; abdominal sternum VII, marginal setae male, one pair; female, two pairs.

Head.—Genae smooth, not rugose. Eyes flattened slightly.

Prothorax.—Pronotum with anterior bead complete; lateral beads present. Posterolateral impressions impunctate, or sparsely punctate; angles broadly rounded. Lateral margins not sinuate, beaded.

Pterothorax.—Mesepisternum impunctate. Metepisternum shortened slightly, lateral margin slightly longer than anterior margin.

Elytra.—Surface smooth. Elytron, humerus obliquely narrowed; elytron, lateral margin narrowly rounded. Apex spinose, shorter; sutural apex angulate. Interneurs 2–6 continuous, shallow, completely punctate. Discal and umbilical setigerous punctures foveate.

Hind Wings.—Brachypterous.

Legs.—Tarsomeres 1–3 of mid- and hind tarsi sulcate. Fore tarsomere 4, inner lobe longer than basal portion; hind tarsomere 4, outer lobe as long as basal portion.

Ovipositor.—(Ball and Shpeley, 1992:406, fig. 2a–f) Stylomere 2 form 1, ensiform setae marginal.

Habitat

Probably understory vegetation in dry primary evergreen montane forest (Ball and Shpeley, 1992:407).

Chorological Affinities

The ranges of *O. donato* and its close relatives (*O. championi* and *O. iris*) are nonoverlapping. The range of *O. donato* probably is overlapped by the ranges of six other species of *Onypterygia* (Ball and Shpeley, 1992:407).

Phylogenetic Relationships

See this topic for *O. iris* above.

Material Examined

We have seen the holotype of *O. donato* only.

Onypterygia chrysura Bates
(Fig. 65, 82A–C, 107)

Onypterygia chrysura, Bates 1882:131. Lectotype (here designated) female, labelled: “TYPE/ H. T.” [circular, ringed with red]; S. Geronimo./ Guatemala/ Champion”; “B.C.A. Col. I.1/ Onypterygia/ chrysura/ Bates”; “Onypterygia/ chrysura/ Bates” [handwritten, in Bates’ hand]; “LECTO-TYPE” [circular, ringed with purple]; “♀ BMNH/LECTOTYPE/det. D. R. Whitehead [red un-

derline]/ *Onypterygia/ chrysura*/ Bates/ det. D. R. Whitehead" (BMNH). Paralectotypes (here designated), three additional specimens, similarly labelled (BMNH).

Type Locality

San Geronimo. Baja Verapaz, Guatemala (here restricted).

Diagnostic Combination

With character states of the *O. fulgens* group, restricted as follows. Pronotum with two pairs of lateral marginal setae; lateral margins wide, not beaded, hind angles obtuse but evident. Elytra metallic green, not vittate, with or without cupreous reflection laterally; interval 3 with three nonfoveate setigerous punctures, apex obtusely angulate, sutural interval angulate but not distinctly denticulate. Sternum VII of female with two pairs of posterior marginal setae. Internal sac of male genitalia long, with long row of setae, without spinose sclerites.

Description

With diagnostic combination of *O. chrysura* and the following.

Measurements and Proportions.—TL large (11.2 mm), WP/WH intermediate (1.30), LP/WP intermediate (0.90), WP/WPb intermediate (1.20), LE/WE intermediate (1.70).

Color.—Head dark green. Antennae with basal articles partially metallic. Pronotum dark green. Elytra with disc concolorous, bright green. Femora metallic, partially black.

Microsculpture, Mesh Pattern.—Head, microlines partially effaced, isodiametric; pronotum, transverse; elytra, isodiametric.

Chaetotaxy.—Pronotum, lateral setae two pairs; elytron, discal setae three; dorsoapical portion of hind femur with setae, or without setae; abdominal sterna IV–VI one pair of setae each; abdominal sternum VII, marginal setae male, one pair; female, two pairs.

Head.—Genae smooth, not rugose. Eyes moderately prominent, convexity average.

Prothorax.—Pronotum (Fig. 65). Anterior bead complete; lateral beads absent. Posterolateral impressions impunctate, or sparsely punctate; angles broadly rounded. Lateral margins not sinuate.

Pterothorax.—Mesepisternum partially punctate. Metepisternum elongate.

Elytra.—Surface smooth. Elytron, humerus broadly rounded; elytron, lateral margin narrowly rounded. Apex angulate; sutural apex angulate. Interneurs 2–6 continuous, shallow, completely punctate. Discal and umbilical setigerous punctures not foveate.

Hind Wings.—Macropterous.

Legs.—Tarsomeres 1–3 of mid- and hind tarsi sulcate. Fore tarsomere 4, inner lobe longer than basal portion; hind tarsomere 4, outer lobe as long as basal portion.

Male Genitalia.—Median lobe, in dorsal aspect (Fig. 82A) with apical portion short, apex broadly rounded, lobate; in left lateral aspect (Fig. 82B), apical portion narrow, apex acute. Internal sac (Fig. 82C) markedly elongate; basal and preapical lobes absent; armature, setose spines on ventral surface.

Ovipositor.—Stylomere 2 form 2.

Variation

Throughout the range of this species, the number of dorsoapical setae of the hind femur varies from 0 to 3. The Costa Rican specimens are distinctive in that the cupreous reflection of the elytra is absent or slight, the interneurs are more distinctly punctulate, and the apex of the median lobe is slightly less lobate. Two females, one collected near Danlí, and the other in Parque Nacional La Muralla, Honduras, are duller green overall, and with the microlines of the elytra more distinct than normal for the species.

Habitat

Onypterygia chrysura probably lives in wet montane tropical forest, at middle altitudes.

Geographical Distribution

This species is known from localities in southern Mexico, Guatemala, Honduras, and Costa Rica (Fig. 107). The absence of specimens from El Salvador and Nicaragua probably reflects lack of collecting in these countries.

Chorological Affinities

The range of *O. chrysura* is overlapped by the ranges of most species of the *O. famini*, *pusilla*, *angustata*, and *fulgens* species groups.

Material Examined

We have seen 17 specimens of *O. chrysura* from the following localities.

MEXICO. Chiapas: Ciudad Cuauhtémoc (UASM). **COSTA RICA. Puntarenas:** Monteverde—1 male, VI.4–6.1980, J. E. Wappes (JEWG); 1 female, V.28–31.1979, J. M. & B. A. Campbell (CNCI); 1 male, 1400 m, V.10.1989, J. Ashe, R. Brooks, R. Leschen (SEMC); 1 male, same, V.23.1989 (SEMC); 1 male, same, H. & A. Howden (UASM); 1 female, San Luis, R. B. Monteverde, VIII.1992, L-N-250850, 449250, Z. Fuentes (INBC); 1 female, 2 km S Santa Elena, 1300 m, VI.2.1979, H. & A. Howden (UASM). **San José:** 1 female, San José, VI.27.1925, Schmidt (CMNH). **GUATEMALA. Baja Verapaz:** San Geronimo (BMNH). **Escuintla:** Zapote (BMNH). **Quetzaltenango:** Cerro Zunil (BMNH). **HONDURAS. Olancha:** Parque Nacional La Muralla, MV + UV light, V.24.1995, R. H. Turnbow (RHTC). **Paraíso:** 1 male, 35 km E Danlí, 700 m, U-V light VI.10.1994, H. & A. Howden (UASM).

Onypterygia kathleenae, new species

(Fig. 11A, B; 66; 83A, B; 102; 107)

Type Material

Six specimens, labelled as follows. Holotype male, "MEX. Oaxaca 16.9/mi.s. Valle/Nacional 3600'/VIII.14–15.65"; "George E. Ball/D. R. Whitehead/collectors" (USNM). Allotype female: "MEXICO Oaxaca/16.9 mi. s. Valle/Nacional, 3600'/V.4–5.1966"; "George E. Ball/D. R. Whitehead/collectors" (USNM). Four paratypes. Female, labelled same as allotype (UASM). Female, "MEXICO/Oaxaca/Km 87/Tuxtepec/Oaxaca/28-V-87/F Arias" (UNAM). Male, "MEXICO: Chiapas Mu-/nicipio de Angel Al-/bino Corzo (Jalte-/nango), above Finca/Custepec,/1371 m 11.VIII.1981/D. E. & P. M. Breedlove"; "♂ gen. drawn/D. Hollingdale/1991" (CASC). Female, "MEXICO: Chiapas, Mu-/nicipio de Angel Al-/bino Corzo (Jalte-/nango) montane rain/forest above Finca/Custepec,/1371 m 24.VI.1981/D. E. & P. M. Breedlove"; "PN drawn/D. Hollingdale/1991 (CASC). Female, "GUAT. Zacapa Sierra/de las Minas, 20.3/km w. Teculután, 21.8/km n. trop. mont. for./1800–1900 m beating/veg. 91-34 8.VI.1991"; "H. F. Howden GUATEMALA EXPED. 1991"; "G. E. and K. E. Ball/D. Shpeley/collectors" (UASM).

Type Locality

27.2 km south of Valle Nacional, Oaxaca, Mexico.

Specific Epithet

This species is named in honor of Kathleen E. Ball, collector of one of the paratypes, in recognition of her numerous contributions to elucidating the carabid fauna of Mexico.

Diagnostic Combination

With character states of the *O. fulgens* species group, restricted as follows. Dorsal surface metallic green. Pronotum with two pairs of lateral marginal setae, posterolateral angles rounded, lateral margins beaded narrowly. Elytra (Fig. 11A, B) acuminate, each with long apical spine. Adults of this species resemble those of *O. exeuros*. For details see "Diagnostic Combination" for that species, below.

Description

With diagnostic combination of *O. kathleenae* and the following.

Measurements and Proportions of Holotype.—TL intermediate (10.5 mm), WP/WH high (1.26), LP/WP intermediate (1.12), WP/WPb high (1.47), LE/WE high (2.05).

Color.—Head dark green. Antennae with antennomere 1 bicolored; apical antennomeres rufous.

Palpi rufopiceous. Pronotum dark green. Elytra with disc concolorous, bright green. Femora bicolored, black and rufous; tibiae and tarsi rufous.

Microsculpture, Mesh Pattern.—Head, microlines partially effaced, isodiametric; pronotum, transverse; elytra, transverse.

Chaetotaxy.—Pronotum (Fig. 66), lateral setae two pairs; elytron, discal setae two; dorsoapical portion of hind femur without setae; abdominal sterna IV–VI one pair of setae each; abdominal sternum VII, marginal setae male, two or more pairs; female, three or more pairs.

Head.—Genae smooth, not rugose. Eyes flattened slightly.

Prothorax.—Pronotum (Fig. 66). Anterior bead complete; lateral beads present. Posterolateral impressions impunctate, or sparsely punctate; angles broadly rounded. Lateral margins not sinuate. Posterolateral pair of setigerous punctures at posterolateral angles, on bead.

Pterothorax.—Mesepisternum partially punctate. Metepisternum elongate.

Elytra.—Surface smooth. Elytron (Fig. 11A, B), humerus broadly rounded; elytron, lateral margin narrowly rounded. Apex acuminate, spine longer than average (cf. Fig. 11A); sutural apex rounded. Interneurs 2–6 discontinuous, series of small punctures, completely punctate. Discal and umbilical setigerous punctures foveate.

Hind Wings.—Macropterous.

Legs.—Tarsomeres 1–2 of middle and hind tarsi sulcate. Fore tarsomere 4, inner lobe longer than basal portion; hind tarsomere 4, outer lobe longer than basal portion.

Male Genitalia.—Median lobe in dorsal aspect (Fig. 83A) with apical portion very short; apex narrowly rounded; in left lateral aspect (Fig. 83B) apical portion broader than in *O. exeuros*, apex acute. Internal sac, moderately elongate; basal and preapical lobes absent; armature absent, but surface with numerous enlarged microtrichia.

Ovipositor.—(Fig. 102) Stylomere 2 form 3.

Habitat

Specimens were collected in tropical montane rain forest at altitudes of 900 to 1900 m.

Geographical Distribution

The range of this species extends from Oaxaca, on the Atlantic Versant of Mexico to the highlands of Guatemala (Fig. 107).

Chorological Affinities

This species is allopatric with reference to its putative adelphotaxon, *O. exeuros*, n. sp., although the Oaxacan localities for the two species are only a few kilometers apart. The range of *O. kathleenae* is overlapped by the ranges of several other species of the *O. fulgens* group, by *O. perissostigma*, and by species of the *famini*, *pusilla*, and *angustata* groups.

Phylogenetic Relationships

Although adults of this species and *O. exeuros* differ markedly in size, they are allopatric in geographical distribution and are strikingly similar in form of elytral apices, in lacking armature from the internal sac of the male genitalia, and in general habitus. On the basis of these considerations, we postulate that *O. kathleenae* and *O. exeuros* are adelphotaxa.

Material Examined

We have seen the type series of *O. kathleenae* only; for details see above.

Onypterygia exeuros, new species (Fig. 15, 67, 107)

Type Material

Seven specimens, labelled as follows. Holotype male, "MEX: Oaxaca/5 mi. SW Esperanza/4 July 1982/R. S. Miller colr"; "♂ Genitalia dissected/& lost/geb-1991" (CUIC). Allotype female, labelled same as holotype (CUIC). Paratypes, five, three (male and two females) labelled same as holotype (CUIC). Female,

"MEX: OAXACA 5 mi/SW La Esperanza/04 Jul 1982/M. A. Ivie colr" (CUIC). Female, "MEXICO/Oaxaca/Km. 87/Tuxtepec-/Oaxaca/28-v-87/F. Arias" (UNAM).

Type Locality

Eight km southwest of Esperanza, Oaxaca, Mexico. This locality is close to the type locality of *O. striblingi*, n. sp.

Specific Epithet

A Greek word, *exeuros*, used as a noun in apposition. It means ending in a tail or point, and refers to the acuminate elytral apices characteristic of this species.

Diagnostic Combination

With character states of the *O. fulgens* species group, restricted as follows. Adults of this species are much like those of *O. kathleenae*, but are substantially larger (length more than 12.5 mm, as opposed to less than 11.0 mm), and lack the anterior pair of pronotal setae. As well, the male genitalia differ: in *O. exeuros*, the median lobe in left lateral aspect is more curved, especially the apical portion. In ventral aspect, the apical portion of the median lobe in *O. exeuros* is narrower than in *O. kathleenae*.

Description

With the diagnostic combination of *O. exeuros*, and the following.

Measurements and Proportions of Holotype.—TL intermediate (12.1 mm), WP/WH intermediate (1.21), LP/WP intermediate (0.89), WP/WPb intermediate (1.16), LE/WE high (1.95).

Color.—Head rufopiceous. Antennae with basal and apical antennomeres piceous-black. Palpi piceous. Pronotum rufopiceous. Elytra with discal pattern concolorous, coppery and green. Femora metallic, partially black; tibiae and tarsi piceous-black.

Microsculpture, Mesh Pattern.—Head, isodiametric; pronotum, transverse; elytra, isodiametric.

Chaetotaxy.—Pronotum, lateral setae one pair, posterior pair absent; elytron, discal setae two or three; dorsoapical portion of hind femur without setae; abdominal sterna IV–VI one pair of setae each; abdominal sternum VII, marginal setae male, two or more pairs; female, three or more pairs.

Head.—Genae rugose, with fine lines. Eyes flattened slightly.

Prothorax.—Pronotum (Fig. 67). Anterior bead complete; lateral beads present. Posterolateral impressions impunctate, or sparsely punctate; angles broadly rounded. Lateral margins not sinuate.

Pterothorax.—Mesepisternum impunctate. Metepisternum elongate.

Elytra.—Surface smooth. Elytron, humerus broadly rounded; elytron, lateral margin slightly sinuate medially. Apex acuminate, longer than average (cf. Fig. 11A, B); sutural apex rounded. Interneurs 2–6 discontinuous, series of small punctures, completely punctate. Discal and umbilical setigerous punctures foveate.

Hind Wings.—Macropterous.

Legs.—Tarsomeres of middle tarsi not sulcate, surface smooth. Hind tarsomere 1 sulcate. Fore tarsomere 4, inner lobe as long as basal portion; hind tarsomere 4, outer lobe as long as basal portion.

Male Genitalia.—Median lobe, apical portion short; apex narrowly rounded. Internal sac, moderately elongate; basal and preapical lobes absent; armature absent, but surface with numerous enlarged microtrichia.

Ovipositor.—(Fig. 15) Stylomere 2 form 2.

Habitat

At the type locality, adults probably were collected from the leaves of planted citrus trees. The citrus grove was in an area that had supported lower montane rain forest.

Geographical Distribution

This species is known only from the Atlantic Versant of Oaxaca (Fig. 107), at an altitude of about 610 m.

Chorological Affinities

As noted above, this species and *O. kathleenae* are allopatric with respect to one another, although their ranges are nearly in contact. Other species near to or overlapping with *O. exeuros* are *O. angustata*, *O. pseudangustata*, *O. striblingi*, *O. pusilla*, and *O. tricolor*.

Phylogenetic Relationships

This species is the putative adelphotaxon of *O. kathleenae*. For details see "Phylogenetic Relationships" for the latter species, above.

Material Examined

We have seen the type series only; for details see above.

Onypterygia polytreta, new species

(Fig. 4A–C; 20; 77; 84A, B; 87; 103; 107)

Type Material

Eight specimens, labelled as follows. Holotype male: "PANAMA Chiriquí/Pr. Cerro Pando/1535 m./24 May 1973/1535 M. G. Ekis" [handwritten]; "♂ + winged"; "ADP/27606"; "♂ gen. drawn/D. Hollingdale/1991" (USNM). Allotype female: labelled same as holotype, except "♀ + winged"; "ADP/27608" (USNM). Six paratypes. Male, labelled same as holotype, except: "ADP/27607" (USNM). Male, labelled same as holotype, except locality label printed, and: "ADP/27605" (USNM). Male and three females, "V. de Chiriquí/M. de Mathan/1901; [male, labelled: "m. 1. and sac/drawn/D. R. Whitehead"] (MNHP).

Type Locality

Cerro Pando, Chiriquí Province, Panama. This mountain, which attains an altitude of 2441 m, is at 80°55'N, 82°34'W, 18 km northwest of Hato del Volcán (Howden and Young, 1981:6).

Specific Epithet

From Greek, *polytreto*s, meaning full of holes, in reference to the deeply foveate elytra of adults of this species.

Diagnostic Combination

With character states of the *O. fulgens* species group, restricted as follows. Adults of *O. polytreta* differ from all other *Onypterygia*, except *O. crabilli*, n. sp., by having deep foveae on intervals 3, 5, and 7, and from most others except *O. hoepfneri* by additional setae on abdominal sterna IV–VI. The peculiar elytral color pattern resembles that of *O. iris* and *O. championi*, but *O. polytreta* differs in lack of anterolateral setae and males differ strikingly in details of the genitalia. For differences from *O. crabilli*, see discussion of the diagnostic combination of that species.

Description

With diagnostic combination of *O. polytreta* and the following.

Habitus.—As in Figure 20.

Measurements and Proportions of Male Paratype.—TL large (14.8 mm), WP/WH high (1.30), LP/WP intermediate (1.38), WP/WPb low (1.18), LE/WE intermediate (1.84).

Color.—Head bright green. Antennae with basal and apical antennomeres piceous-black. Palpi piceous. Pronotum bright green. Elytra with disc bicolored-striped, coppery green. Femora, tibiae, and tarsi piceous to black.

Microsculpture, Mesh Pattern.—Head, isodiametric; pronotum, transverse; elytra (Fig. 4A), slightly transverse.

Chaetotaxy.—Pronotum, lateral setae one pair, anterolateral pair absent; elytron discal setae more

than three; dorsoapical portion of hind femur without setae; abdominal sterna IV–VI more than one pair of setae each; abdominal sternum VII, marginal setae male, two or more pairs; female, three or more pairs.

Head.—Genae smooth, not rugose. Eyes prominent, convexity marked.

Prothorax.—Pronotum (Fig. 77). Anterior bead complete; lateral beads absent. Posterolateral impressions impunctate, or sparsely punctate; angles broadly rounded. Lateral margins not sinuate.

Pterothorax.—Mesepisternum impunctate. Metepisternum elongate.

Elytra.—Surface with prominent discal foveae (Fig. 4B, C), uneven. Elytron, humerus broadly rounded; elytron, lateral margin slightly sinuate medially. Apex acuminate, spine shorter; sutural apex rounded. Interneurs 2–6 discontinuous, series of small punctures, completely punctate. Discal and umbilical setigerous punctures foveate.

Hind Wings.—Macropterous.

Legs.—Tarsomeres 1–3 of middle and hind tarsi not sulcate, surface smooth. Fore tarsomere 4, inner lobe longer than basal portion; hind tarsomere 4, outer lobe as long as basal portion.

Male Genitalia.—Median lobe in dorsal aspect (Fig. 84A), with apical portion short; apex moderately broadly rounded; in left lateral aspect (Fig. 84B), apical portion narrow, dorsal surface curved, apex acute. Internal sac (Fig. 87), markedly elongate; basal and preapical lobes absent; armature with seven spinose sclerites, as follows—two basal (one ventral, one medial), three median (one left lateral, one right lateral, and one ventral), and two apical (one dorsal and one ventral).

Ovipositor.—(Fig. 103) Stylomere 2 form 3.

Geographical Distribution

This species is known only from Chiriquí Province, Panama (Fig. 107).

Chorological Affinities

This species is allopatric in relation to its postulated adelphotaxon, *O. crabilli*, which is known from Costa Rica. The range of *O. polytreta* is overlapped only by the ranges of *O. angustata*, *O. championi*, and *O. tricolor*.

Phylogenetic Relationships

Based on similarities in details of the elytra, in armature of the internal sac of the male genitalia, and on proximity but nonoverlapping of geographical ranges, this species and *O. crabilli* are postulated to be adelphotaxa.

Material Examined

We have seen the type specimens of *O. polytreta* only; for details see above.

Onypterygia crabilli, new species

(Fig. 5A–C; 68; 85A, B; 88; 107)

Type Material

Seven specimens, labelled as follows. Holotype male, “COSTA RICA, PUNTARENAS/ MONTEVERDE/ May 23–27 1987/ E. GIESBERT, COLL” [handwritten] (FSCA). Allotype female, “C. R. Pnt. 1500 m/Reserva de/Monte Verde/ 1–4.VI.1979/J M & B A Campbell” (CNCI). Paratypes, five, as follows. Female, “COSTA RICA: Provin-/cia de Puntarenas, Monteverde Biological/Reserve, at light/15.IX.1990 Norman D. Penny/Cal. Acad. Sc. Coll” (CASC). Female, “Ref. Nac. Fauna Silv./ Tapanti 1150 m Prov./ Cart. COSTA RICA, G./ Mora, F. Quesada, Ene/ 1992, L-N-194000, 559800” (INBC). Female, “Est. Zurqui 500 m antes/ de Tunzel, 1600 m. Prov./ S Jose, COSTA RICA,/ G. Maass. Abr 1991/ L-N-226800, 535200” (INBC). Female, same as previous label, except date: “26 set–oct 1990” (INBC). Male, “Palma, C. R./Aug. 1924”; “Nevermann/Collection/1940” [green paper]; “ADP 57251” (USNM).

Type Locality

Monteverde, Puntarenas Province, Costa Rica.

Specific Epithet

This species is named in honor and in memory of our long-time friend and colleague, the late Ralph E. Crabill, Jr., a noted myriapod specialist, who devoted many years to the classification of North American chilopods.

Diagnostic Combination

With character states of the *O. fulgens* species group, restricted as follows. Like adults of *O. polytreta*, specimens of this species have deep foveae scattered on the disc of the elytra. Unlike *O. polytreta*, however, most of the discal foveae of *O. crabilli* lack setae, and the elytra, rather than green with coppery reflections, are uniformly aeneous, and only females have extra ambulatory setae, and these only on sternum VI. The male genitalia of the two species differ also. See Figures 84A, B; 85A, B; 87; and 88.

Description

With diagnostic combination of *O. crabilli* and the following.

Measurements and Proportions of Holotype.—TL intermediate (12.0 mm), WP/WH low (1.22), LP/WP intermediate (0.75), WP/WPb high (1.42), LE/WE intermediate (1.75).

Color.—Head bronze-green. Antennae with basal and apical antennomeres rufous. Palpi rufopiceous. Pronotum bronze-green. Elytra with discal pattern concolorous; bronze-green, metallic. Femora rufous; tibiae and tarsi rufous.

Microsculpture, Mesh Pattern.—Head, isodiametric; pronotum, transverse; elytra (Fig. 5A), transverse.

Chaetotaxy.—Pronotum, lateral setae one pair, posterior pair absent; elytron—discal setae more than three; dorsoapical portion of hind femur without setae; abdominal sterna IV–V with one pair each; sternum VI with two pairs; abdominal sternum VII, marginal setae, male, two or more pairs; female, three or more pairs.

Head.—Genae smooth, not rugose. Eyes prominent, convexity marked.

Prothorax.—Pronotum (Fig. 68). Anterior bead complete; lateral beads absent. Posterolateral impressions impunctate, or sparsely punctate; angles broadly rounded. Lateral margins not sinuate.

Pterothorax.—Mesepisternum impunctate. Metepisternum elongate.

Elytra.—Surface with prominent discal foveae, uneven. Elytron, humerus broadly rounded; lateral margin broadly rounded. Apex spinose, shorter; sutural apex angulate. Interneurs 2–6 evanescent, completely punctate. Discal and umbilical setigerous punctures (Fig. 5B, C) foveate.

Hind Wings.—Macropterous.

Legs.—Tarsomere 1 of mid- and hind tarsi sulcate. Fore tarsomere 4, inner lobe longer than basal portion; hind tarsomere 4, outer lobe as long as basal portion.

Male Genitalia.—Median lobe in dorsal aspect (Fig. 85A) with apical portion moderately long; apex narrowly rounded; in left lateral aspect (Fig. 85B), apical portion narrow, curved moderately ventrad, apex acute. Internal sac (Fig. 88), moderately elongate; basal and preapical lobes absent; armature of ten spinose sclerites, as follows—four basal (three left lateral, one dorsal), two median dorsal and two preapical (one dorsal, one ventral), and two apical (one dorsal and one ventral).

Ovipositor.—Stylomere 2 form 3.

Habitat

Probably tropical montane forest, at around 1400–1550 m altitude.

Geographical Distribution

This species is known from Costa Rica only (Fig. 107).

Chorological Affinities

This species and its close relative, the Panamanian *O. polytreta*, are allopatric in relation to one another. The range of *O. crabilli* is overlapped by the ranges of *O. angustata*, *O. donato*, *O. chrysura*, *O. quadrispinosa*, *O. scintillans*, and *O. tricolor*. Of these species, *O. donato*, *O. chrysura*, and *O. tricolor* have been collected at or near Monteverde, the type locality of *O. crabilli*.

Phylogenetic Relationships

This species and *O. polytreta* are postulated to be adelphotaxa. For details see "Phylogenetic Relationships" for the latter species.

Material Examined

We have seen the type series of *O. crabilli* only; for details see above.

Onypterygia quadrispinosa Bates

(Fig. 69; 70; 86A, B; 107)

Onypterygia quadrispinosa Bates, 1882:130. Type material, four specimens, as follows. Lectotype (here designated) female, labelled: "TYPE H. T." [circular label ringed with red]; "LECTO-/TYPE" [circular label ringed with purple]; "Cerro Zunil/ 4-5000 ft./ Champion"; "B.C.A. Col.I.1/ Onypterygia/ quadrispinosa./ Bates"; "Onypterygia/ 4 spinosa/Bates" [handwritten]; "♀ BMNH/ LECTOTYPE/ [red underline]/ det. D. R. Whitehead/ Onypterygia.quadrispinosa/ Bates/ det. D. R. Whitehead" (BMNH). Paralectotypes, two males, one female, with same locality and determination labels as lectotype.

Type Locality

Cerro Zunil, Department of Quetzaltenango, Guatemala.

Diagnostic Combination

With character states of the *O. fulgens* species group, restricted as follows. *Onypterygia quadrispinosa* is the only species with coppery-green elytra having sutural denticulae as well as denticulate apices; the denticulae are produced as short spines. In this respect, *O. quadrispinosa* is similar to *O. fulgens*, but the apex of the latter is as a whole less produced, less markedly sinuate subapically, and the elytra are predominantly metallic green or blue.

Despite Bates's (1882:130) observations, the elytra are not markedly striped. From above, they appear mainly maroon, with sutural intervals, margins, and preapical calli metallic green; from behind, the color is mainly metallic green, with a maroon band across the preapical calli.

Description

With diagnostic combination of *O. quadrispinosa*, and the following.

Measurements and Proportions of Male Paralectotype.—TL large (14.2 mm), WP/WH low (1.26), LP/WP intermediate (0.83), WP/WPb intermediate (1.22), LE/WE high (2.02).

Color.—Head coppery green. Antennae with basal and apical antennomeres piceous to black. Palpi piceous. Pronotum coppery green. Elytra with disc concolorous, coppery green. Femora, tibiae, and tarsi piceous to black.

Microsculpture, Mesh Pattern.—Head, microlines partially effaced, isodiametric; pronotum, microlines effaced, surface smooth; elytra, transverse.

Chaetotaxy.—Pronotum, lateral setae one pair, posterior pair absent; elytron—discal setae two or three; dorsapical portion of hind femur without setae; abdominal sterna IV–VI one pair of setae each; abdominal sternum VII, marginal setae—male, two or more pairs; female, three or more pairs.

Head.—Genae smooth, not rugose. Eyes prominent, convexity marked.

Prothorax.—Pronotum (Fig. 69, 70). Anterior bead incomplete; lateral beads present. Posterolateral impressions impunctate, or sparsely punctate; angles broadly rounded. Lateral margins not sinuate.

Pterothorax.—Mesepisternum partially punctate. Metepisternum elongate.

Elytra.—Surface smooth. Elytron, humerus broadly rounded; lateral margin slightly sinuate medially. Apex denticulate; sutural apex denticulate. Interneurs 2–6 discontinuous, series of small punctures, impunctate. Discal and umbilical setigerous punctures foveate.

Hind Wings.—Macropterous. Wedge cell elongate.

Legs.—Tarsomeres 1–3 of middle and hind tarsi sulcate. Fore tarsomere 4, inner lobe longer than basal portion; hind tarsomere 4, outer lobe as long as basal portion.

Male Genitalia.—(Fig. 86A, B) Median lobe in dorsal aspect (Fig. 86A) with apical portion short, apex narrowly rounded. Internal sac, markedly elongate; basal and preapical lobes absent; armature absent.

Ovipositor.—Stylomere 2 form 3.

Habitat

Probably this species inhabits montane tropical forest.

Geographical Distribution

This species is known from two widely separated areas: the Pacific Versant of Guatemala, and the Atlantic and Pacific versants of Costa Rica (Fig. 107).

Chorological Affinities

The range of *O. quadrispinosa* is overlapped by the ranges of many species of *Onypterygia*, included in the *famini*, *pusilla*, *angustata*, and *fulgens* species groups. Other species collected on Cerro Zunil, and possibly syntopic there with *O. quadrispinosa* are *O. chrysura* and *O. longispinis*. Geographical relations between *O. quadrispinosa* and its putative adelphotaxon, *O. scintillans*, n. sp., cannot be specified, because the location of the latter is not known.

Phylogenetic Relationships

The putative adelphotaxon of *O. quadrispinosa* is *O. scintillans*, n. sp., based on shared character states of angulate or acuminate sutural apices, and long internal sac of the male genitalia that is without spinose sclerites or with only one.

Material Examined

In addition to the type series, we have seen three specimens of *O. quadrispinosa*, all from Costa Rica, as follows.

Alajuela: 1 female, R. San Lorencito, R. F. San Ramon, 5 km N Colonia Palmarena, 900 m, L-N-244500, 470700, VI.13–18.1993 (INBC). **Cartago:** 1 female, La Suiza de Turrialba, 1923, Pablo Schild (CMNH). **Puntarenas:** Alajuela, Peñas Blancas XII.1–12.1986, E. Cruz (UASM).

Onypterygia scintillans, new species (Fig. 89A, B; 107)

Type Material

One specimen only. Holotype male, labelled: “Holo-type” [circular label, ringed with red]; “Col. Zeledon/ [illegible writing]/X11.25”; “Nevermann/Collection/1940” [green paper]; “PN ♂ gen/drawn/D. Hollingdale/1990” (USNM).

Type Locality

The labelling is inadequate to establish the place of the type locality. Since the specimen was in the Nevermann collection, we assume that it was taken in Costa Rica. We have been unable to locate a gazetteer or map reference to “Col. [= Colonia?] Zeledon.”

Specific Epithet

A Latin present participle, *scintillans*, of the verb *scintillare*, meaning to sparkle; in allusion to the gleaming dorsal surface of the holotype.

Diagnostic Combination

With character states of the *O. fulgens* species group, restricted as follows. Similar to *O. quadrispinosa* in size and most other features, the holotype of *O. scintillans* has its elytral apices rounded rather than angulate.

Description

With diagnostic combination of *O. scintillans* and the following.

Measurements and Proportions of Holotype.—TL moderate (13.0 mm), WP/WH low (1.33), LP/WP intermediate (0.74), WP/WPb intermediate (1.31), LE/WE high (1.87).

Color.—Head dark green. Antennae with basal and apical antennomeres rufous. Palpi piceous. Pronotum dark green. Elytra with disc concolorous, dull green. Femora, tibiae, and tarsi rufous.

Microsculpture, Mesh Pattern.—Head, isodiametric; pronotum, microlines effaced, surface smooth; elytra, isodiametric.

Chaetotaxy.—Pronotum, lateral setae one pair, anterior pair absent; elytron—discal setae two; dorsoapical portion of hind femur without setae; abdominal sterna IV–VI one pair of setae each; abdominal sternum VII with two pairs of marginal setae.

Head.—Genae smooth, not rugose. Eyes prominent, convexity marked.

Prothorax.—Pronotum. Anterior bead incomplete; lateral beads present, posteriorly only. Postero-lateral impressions impunctate, or sparsely punctate; angles broadly rounded. Lateral margins not sinuate.

Pterothorax.—Mesepisternum partially punctate. Metepisternum elongate.

Elytra.—Surface smooth. Elytron, humerus broadly rounded; elytron, lateral margin slightly sinuate medially. Apex rounded; sutural apex angulate. Interneurons 2–6 discontinuous, series of small punctures. Discal and umbilical setigerous punctures foveate.

Hind Wings.—Macropterous.

Legs.—Tarsomeres of middle and hind tarsi not sulcate, surface smooth. Fore tarsomere 4, inner lobe longer than basal portion; hind tarsomere 4, outer lobe as long as basal portion.

Male Genitalia.—Median lobe in dorsal aspect (Fig. 89A) with apical portion moderately long, apex narrowly rounded; in left lateral aspect (Fig. 89B), apical portion slender, apex acute. Internal sac, markedly elongate; basal and preapical lobes absent; armature one spinose sclerite.

Ovipositor.—Unknown.

Habitat and Geographical Distribution

Unknown, other than that the type locality probably is in Costa Rica (Fig. 107).

Chorological Affinities

Unknown.

Phylogenetic Relationships

This species is the putative adelphotaxon of *O. quadrispinosa*. See this topic for the latter species, above.

Material Examined

We have seen the holotype of *O. scintillans* only; for details see above.

Onypterygia fulgens Dejean

(Fig. 11F–H; 71; 90A, B; 91A, B; 92A, B; 97A, B, 104; 108)

Onypterygia fulgens Dejean, 1831:348. Lectotype (here designated) female, labelled: "Mexique/ fulgens mihi" [green paper]; "Chevrolat" [green paper]; "Ex Musaeo/Chaudoir" [red print] (MNHP). Castelnau, 1840:42. Bates, 1882:131. Heyne, 1895:25.

Onychopterygia fulgens; Gemminger and Harold, 1868:384. Chaudoir, 1878:275.

Onypterygia thoreyi Mannerheim, 1844:869. Lectotype (here designated) male labelled "Acapulco" [script]; "Thoreyi Mannerh." [script]; "Ex Musaeo/Thorey" (MNHP). Bates, 1882:131. Heyne, 1895: 25. New synonymy.

Onychopterygia thoreyi; Gemminger and Harold, 1868:384. Chaudoir, 1878:275.

Type Locality

For typical *O. fulgens*, the type area is Mexico, with type locality here restricted to Orizaba, Veracruz, Mexico.

The type locality for *O. thoreyi* is Acapulco, Guerrero, Mexico.

Diagnostic Combination

With character states of the *O. fulgens* species group, restricted as follows. Pronotum without marginal setae; also, elytra metallic green or blue, with or without coppery reflections, elytra apically with apex and apex of suture angulate, and sternum VII of females with more than two pairs of posterior marginal setae.

Description

With diagnostic combination of *O. fulgens* and following.

Measurements and Proportions.—TL intermediate to large (10.5–16.5 mm), WP/WH low (1.18), LP/WP high (0.84), WP/WPh intermediate (1.26), LE/WE high (1.74).

Color.—Head bright green. Antennae with basal antennomeres partially metallic; apical antennomeres piceous-black. Palpi piceous. Pronotum bright green. Elytra with disc concolorous, bright green to dark blue, laterally color of disc or with bright coppery reflections. Femora metallic, partially black; tibiae and tarsi piceous to black.

Microsculpture, Mesh Pattern.—Head, isodiametric; pronotum, isodiametric; elytra, isodiametric.

Chaetotaxy.—Pronotum, lateral setae absent; elytron—discal setae three; dorsoapical portion of hind femur without setae; abdominal sterna IV–VI one pair of setae each; abdominal sternum VII, marginal setae—male, two or more pairs; female, three or more pairs.

Head.—Genae rugose, with fine lines. Eyes prominent, convexity marked.

Prothorax.—Pronotum (Fig. 71). Anterior bead incomplete; lateral beads absent. Posterolateral impressions impunctate, or sparsely punctate; angles broadly rounded. Lateral margins not sinuate.

Pterothorax.—Mesepisternum partially punctate. Metepisternum elongate.

Elytra.—Surface smooth. Elytron, humerus broadly rounded; lateral margin narrowly rounded. Apex denticulate; sutural apex denticulate. Interneurs 2–6 continuous, moderately deep, punctate for part of length. Discal and umbilical setigerous punctures not foveate.

Hind Wings.—Macropterous.

Legs.—Tarsomeres 1–3 of middle and hind tarsi sulcate. Fore tarsomere 4, inner lobe longer than basal portion; hind tarsomere 4, outer lobe as long as basal portion. Climbing setae (cs), setation of tarsomere 5 (vs), and pectination (p) of claws as in Figure 11F–H.

Male Genitalia.—Median lobe in dorsal aspect (Fig. 90A–92A) with apical portion short to very short, apex acute; in left lateral aspect (Fig. 90B–92B), apical portion narrow, more or less parallel sided, apex acute. Internal sac (Fig. 97A, B) markedly elongate, without basal and preapical lobes; armature with about 14 spinose sclerites, as follows—two basal-dorsal (one ventral, one right-lateral), six premedial dorsal, six preapical (three left-lateral and three right-lateral).

Ovipositor.—(Fig. 104) Stylomere 2 form 3.

Variation

This species varies notably in color, the junior synonym, *O. thoreyi*, designating a geographically distinctive form of *O. fulgens*. We found no significant variation in either male genitalia or female ovipositor; the number of spinose sclerites on the internal sac varies, but without marked geographical correlation.

All specimens examined from Central America, Chiapas (107) and Oaxaca (9), and nearly all from Veracruz (100) are typical *O. fulgens*: elytra shiny, intervals flat, color bright metallic green with coppery reflections, at least apically; legs uniformly dark. The sole specimen from Minatitlán, Veracruz, is typical "*O. thoreyi*": elytra comparatively dull, intervals convex, no coppery reflections; legs red. One specimen in a series of otherwise typical *O. fulgens* from 6.2 mi (10 km) NW Jalapa has reddish legs, but normal coppery reflecting elytra.

Six specimens, from San Luis Potosí, match typical *O. fulgens* except that only one has distinctly coppery reflecting elytra; since the elytra of this series tend to be shiny dark blue rather than green, they resemble the blue variety recorded by Chaudoir (1878:275) and Bates (1882:131) from Cuernavaca, Morelos. We found no recent specimens of the noncoppery, shiny, dark blue, black-legged Cuernavaca form of *O. fulgens*, but we have seen old specimens in European collections. Most specimens from Morelos are red-legged, typical "*O. thoreyi*," except one black-legged *O. fulgens*.

A broad hybrid zone between *O. fulgens* "*thoreyi*" and nominotypical *O. fulgens* is in Guerrero (44 specimens) and Morelos (39 specimens): 12 specimens have coppery reflections as in typical *O. fulgens*, but seven of them are red legged; and 71 have noncoppery elytral reflections, as in *O. fulgens* "*thoreyi*," but only 58 of them have red legs.

North of the Río Balsas in Guerrero (Apipilulco, Buena de Cuellar, Iguala, and Taxco) and Morelos, 59 specimens have red legs and noncoppery-reflecting elytra (91%), five have black legs and noncoppery-reflecting elytra (7%), and one has red legs and coppery-reflecting elytra (2%). South of the Río Balsas in Guerrero

(Chilpancingo, Mazatlán, and Omiltemi), 21 specimens have noncoppery-reflecting elytra, and 13 of these are red legged (40%) and eight are black legged (25%); and 11 have coppery-reflecting elytra, of which six are red legged (19%) and five are black legged (16%). Chilpancingo is the only sampling area represented both by a definite mix of coppery- and noncoppery-reflecting elytra (ratio about 2:1) and also by numerous specimens that combine coppery-reflecting elytra with pale legs. In the Chilpancingo area, the ratio of red-legged to dark-legged is about 3:2, in contrast to about 9:1 toward Taxco and into Morelos.

Specimens from the following areas are all *O. fulgens* "thoreyi," with noncoppery-reflecting green or blue elytra: localities north of the Río Grande de Santiago—Chihuahua and Sonora: four specimens, all red legged. Sinaloa: 46 red legged (32%) and 98 black legged (68%). Localities south of the Río Grande de Santiago—Nayarit and northwestern Jalisco (Plan de Barranca and Magdalena), 41 red legged (38%) and 65 black legged (62%); 23 km S Tepic, Nayarit, 30 red legged (50%) and 30 black legged (50%); eastern Jalisco (Ajijic, Guadalajara), near Río Santiago headwaters, 68 red legged (67%) and 34 black legged (33%); and Colima and southwestern Jalisco (Casimiro Castillo, La Huerta, Puerto Vallarta, and Talpa de Allende), 16 red legged (48%) and 17 black legged (52%).

Thus, within *O. fulgens* "thoreyi," there is a cline in leg color, with red leggedness increasing from about 32% in Sinaloa to about 90% around Cuernavaca, but the red-legged specimens from the Río Mayo in Chihuahua and Sonora may represent a population discontinuous from that in Sinaloa. In the Chilpancingo area of Guerrero, where red-legged *O. fulgens* "thoreyi" meet black-legged nominotypical *O. fulgens*, numerous intermediates occur (Fig. 108, white diamond-shaped marks). In contrast, there is little evidence that *O. fulgens* "thoreyi" readily hybridizes with eastern populations of *O. fulgens*; the similar and apparently scarce blue forms of *O. fulgens* from Morelos and San Luis Potosí might represent such hybridization, but these darkly colored forms are unlike the hybrid forms in Guerrero.

The single specimen of typical *O. fulgens* "thoreyi" from Minatitlán, Veracruz, might be an erroneous record, or it may represent a population of true *O. fulgens* "thoreyi" inside the range of nominotypical *O. fulgens*. There may have been a partial development of reproductive isolation between *O. fulgens* "thoreyi" and nominotypical *O. fulgens* (perhaps represented by character displacement in leg color near the point of contact between them) which broke down subsequently in the south and southwest, but not in the east.

Habitat

Adults of *O. fulgens* live on vegetation in forests of various types, ranging in altitude from near sea level to about 2500 m. During the period May through September, many specimens have been taken at night using UV light traps; during the day, they are obtained by sweeping or beating vegetation. From December through May, they are commonly collected from bromeliads. Specimens have been collected on the ground, but in tree-fall litter.

Geographical Distribution

The range of this species extends from southern Sonora and Chihuahua in the west to southern San Luis Potosí in the east, southward to Costa Rica, with a population in Venezuela that is perhaps isolated from the Middle American part of the species' range (Fig. 108). Nominotypical *O. fulgens* ranges north to Ve-

racruz and Oaxaca, *O. fulgens* "thoreyi" ranges from Sonora south to Michoacán and Jalisco, and intermediates occur in Guerrero and Morelos.

Chorological Affinities

The range of this species overlaps the ranges of all other species groups of *Onypterygia*, and as well the ranges of the species to which it seems to be most closely related: *O. tricolor*, *O. hoeppferi*, and *O. sallei*.

Material Examined

We have seen 1392 adults of this species, collected in the following localities.

MEXICO. Chiapas: 11.5 km S Amatenango del Valle (UASM); Chiapa de Corzo (USNM); jct. Hwy. 190 & 195, ne. Chiapa de Corzo (UASM); 1 female, 2 km S Chicoasén, rd. to Mirador, H. F. Howden, VI.18.1989 (UASM); 1 male, Cinco Cerros, Km 30 on Hwy. 190, 1500 m, V.8.1989, H. F. Howden (UASM); 1 male, same, VI.9.1990, H. & A. Howden (UASM); 1 male, El Chorreadero, 8.8 km E Chiapa de Corzo, VI.22.1990, R. H. Turnbow (RHTA); 52.3 km E Comitán, 8 km N. Frontera Comalapa; 1 male, 7 km NE Huixtla, 305 m, X.7.1972 (CASC); 1 specimen, 11 km S Jitotol, bromeliads, V.5.1966, Ball and Whitehead (UASM); 1 female, Km 20, Motozintla-Comitán Hwy., 900 m, VII.8.1988, A. Cadena, L. Cervantes (UNAM); 3 males, Nuevo Amatenango, 1000 m, VII.8.1988, A. Cadena, L. Cervantes (UNAM); 1 female, 9.8 km N. Ocosingo, Chincultic, VI.20.1990, R. H. Turnbow (RHTC); 1 female, Municipio Oxchuc, Rancho San Ramón, VII.12.1975, T. A. Hubbell (U. Ariz. Coll); 14.8–20.1 km N. & 16 km W Ocozacoautla (UASM); Palenque (UASM); 2 males, Parque Nacional El Aguacero, 16 km W Ocozacoautla, V.9.1989, H. F. Howden (UASM); 2 females, same, VI.12.1991, B. Ratcliffe, J. S. Ashe, M. Jameson (SEMC); 1 female, Parque Laguna Belgica, flight intercept trap, 970 m, VI.08.1991, J. S. Ashe (SEMC); Parque Nacional Montebello, Laguna Pojoj, VI.12.1989, H. F. Howden (UASM); 5 males, 3 females, Parque Nacional Sumidero, 1100 m, V.25.1990, H. F. Howden (UASM); 1 male, same, V.26.1990, B. D. Gill (CMNC); 1 female, same, V.29.1990, H. & A. Howden (UASM); 1 male, 1 female, same, Coyota Mirador, 1700 m, VI.10.1989, H. F. Howden (UASM); 3 males, Parque Nacional Sumidero, VI.1–12.1991, B. Ratcliffe, J. S. Ashe, M. Jameson (SEMC); 1 male, same, 700 m, flight intercept trap, J. S. Ashe (SEMC); 8 specimens, Pueblo Nuevo, 1547 m, bromeliads, V.25.1966, Ball and Whitehead (UASM); 5.0 km S Pueblo Nuevo; 1 specimen, 13 km E Rizo de Oro, Rte. 190 (UASM); 1 male, Ruinas Chincultic, 1500 m, VI.3.1990, H. & A. Howden (CMNC); 2 females, same, rd. to Montebello, VI.12.1989, H. F. Howden (UASM); 13.8 km E, 23.8 km SE, & 43.4 km W San Cristóbal de las Casas (UASM); 1 specimen, E slope Sierra de Colmena, nr. La Caverna, Arroyo Santa Maria, G. E. Ball, K. E. Ball, and P. Meyer (UASM); 27.4 km SE Teopisca (UASM); 3 males, km 54, Tuxtla Gutiérrez-Villa Flores, 530 m, VII.12.1988, A. Cadena, L. Cervantes (UNAM); 2 males, 45 km E Tuxtla Gutiérrez, 1400 m, V.28.1990, H. & A. Howden (UASM); 1 female, 18 km W Tuxtla Gutiérrez, X.23.1988, R. H. Turnbow (RHTC); 21.6 km W, 17 km W, 32.2 km S Tuxtla Gutiérrez; 1 ex., Yaxoquintela, 16°58'N, 91°47'W, 560 m, VIII.21.1978, J. E. Rawlins (CMNH); same, IX.17.1978. **Chihuahua:** El Limón, Río Mayo; Gusa-remos, Río Mayo (CASC). **Colima:** Colima (UASM, USNM); 1 male, 20 km NE Colima, VII.17.1990, J. E. Wappes (JEW); 20.8 km E Manzanillo (UASM); 1 female, 14 km E Minatitlán, VI.17.1990, J. E. Wappes (JEW); Mt. Colima; Tecuiztlan. **Distrito Federal:** Mexico (USNM). **Durango:** Ventanas (= Villa Corona; Selander and Vaurie, 1962). **Guerrero:** Apipilulco (USNM); 5.3 km N. rd. to Buenavista de Cuellar; Chilpancingo (FSCA, USNM); 29 km S & 35.4 km N. Chilpancingo (CNCI); 1 male, 1 female, km 95, Coyuca-Zihuatanejo, VII.25.1985, F. Arias, R. Barba (UNAM); 6 specimens, 18 km S El Paraíso, 900 m, VII.5.1982, J. E. Rawlins (CMNH); 12.9 km E Iguala; 1 female, 16 km NW Iguala, 1160 m, IX.12–19.1982, J. A. Chemsak (CISC); Ixcuinatoyac (USNM); 45.1 km S Mazatlán; Omiltemi (UASM); 1 female, Ostotitlán, X.22.1988, H. Brailovsky (UNAM); Rancho Papagaio; 1 specimen, 2.5 km off Rte. 95, road to San Juan Tetelcingo (UASM); Taxco (CNCI); 2 males, 12.9 km N. Taxco, 2000 m, VI.19.1959, H. E. Evans (CUIC); Tepellapa; Tierra Colorada. **Hidalgo:** Ajacuba (CASC). **Jalisco:** 10 males, 7 females, Ajijic (UASM); Ajijic (USNM); 1 male, 6 km S Autlán, VII.16.1990, J. E. Wappes (JEW); Casimiro Castillo (MCPM); 1 female, 0.8 km N. Ciudad Guzmán, X.6.1966, R. F. Smith (CISC); 1 male, 11.7 km S Cocula (UASM); 1 specimen, 8.8 km NW Cocula (UASM); 1 specimen, 15 km W El Texquequite, 1046 m, VI.30.1977, J. E. Rawlins (CMNH); 8 specimens, Guadalajara (CMNH); 1 female, same, VII.13.1959, H. E. Evans (CUIC); 1 male, Guadalajara, Ameca, VIII.1993 (ACCS); 1 male, 2 females, 6.4 km SW Guadalajara, VI.29.1963, J. Doyen (CISC); 31 km N. Guadalajara; 16.4 km NE La Huerta (UASM); 32.2 km NE Magdalena; 4.8 km SE Plan de Barrancas (UCDC); Puerto Vallarta (CASC); 6 males, 6 females, 33.8 km S Puerto Vallarta, on Hwy. 200, 725 m, U-V light, VII.21.1986, S. M. McCleve, P. Jump (UASM); 6.4 & 10.5 km S Talpa de Allende (UASM); 1 female, Tuxpan, 1650 m, VI.24.1979, M. Zunino (ACCS); 17 males, 6

females, Volcán Tequila, 10–14 km SSW Tequila, 2134 m, X.8.1974, D. E. & J. A. Breedlove (CASC). **México:** 4.8 km S Ixtapan de la Sal (UASM); Temascaltepec, Bejucos, H. E. Hinton (MCZC). **Morrellos:** Alpuyeca; 1 male, Cuernavaca, 1524 m, VI.19–29.1959, H. E. Evans (CUIC); 7 km E Cuernavaca (Tejalpa); 14.6 km E Cuernavaca (Cañon de Lobos) (CNCI); 14 specimens, Cañon de Lobos, Km 19, E Cuernavaca, 1120–1375 m, VII.3.1992, C. Bellamy (CMNH); 19.3 km E Cuernavaca; Progreso; Puente de Ixtla; Tequesquitengo (UASM); Xochicalco (UASM); Xochitepec (USNM). **Nayarit:** 3 females, Acaponeta, VII.15.1960, P. H. Arnaud, Jr., E. S. Ross, D. C. Rentz (CASC); Ahuacatlán (UASM); 1 female, vic. Compostela (MCZC); Ixtlán del Río (USNM); La Mesa de Nayar; 3.2 to 14.0 km E San Blas (USNM); San Juan Peyotán; 4 specimens, Tepic, 900 m, VI.27.1977, J. E. Rawlins (CMNH); 60 specimens, 23 km S Tepic, 1077 m, VII.17.1977, J. E. Rawlins (CMNH); 3 males, 30 km SE Tepic, 1270 m, oak–pine forest, U–V light, VII.20–21.1993, S. McCleve, G. E. & K. E. Ball (UASM); 31.1 & 38.6 km se Tepic (UASM). **Oaxaca:** 32.2 km S Juchatengo (UASM); 1 male, Juquila Mixes, dist. de Yautepec, VI.1970, W. S. Miller; 3 males, 3 females, same, VI, VIII & IX.1972; 2 males, 1 female, same, VIII & IX.1974 (CNCI); 2 females, Hwy. 131, 184 km S Oaxaca, V.27–30.1971, D. E. Bright (CNCI); 36 km N. Puerto Escondido (UASM); 4 males, 3 females, San Juan Lachao, Mun. de Juquila, IV.14.1965, G. Halfiter (CNCI); San Miguel Panixtlahuaca; Tehuantepec. **Puebla:** 8.0 km S Izúcar de Matamoros (UASM); Putla. **San Luis Potosí:** 39.7 km E Landa de Matamoros (UASM). **Sinaloa:** 1 male, Choix, VII.5.1968, T. A. Sears (UCDC); 12.9 km NE Concordia (CASC); 9.7 km S Culiacán; 4.8 km E Culiacancito (MCPM); 12.9 km S Elota (UCDC); 25 km E El Palmito; Mazatlán (MCPM); 4 to 16 km N. Mazatlán (MCPM); 1 female, 8 km N. Mazatlán, VII.30.1964, W. C. McGuffin (CNCI); 2 females, same, VIII.5–7.1964, H. F. Howden (CNCI); 1 female, 48 km N. Mazatlán, Microondas El Indio, 412 m, trop. decid. forest, U–V light, 86–16, VIII.6.1986, Ball, Frania, Mulyk (UASM); Venedillo (CASC); 3 males, 2 females, 43.2 km E Villa Union, VII.26.1964, H. F. Howden (CNCI); 1 male, 2 females, 33.6 km E Villa Union, VII.25.1964, H. F. Howden (CNCI). **Sonora:** Charuco, Río Mayo (CASC). **Veracruz:** Coatepec, III.15.1929 (Fall Coll-MCZC); Córdoba (USNM); 1 specimen, 3.9 km NE Coscomatepec, bromeliads, XII.19.1978, G. E. and K. E. Ball (UASM); 18 specimens, jct. Rte. 125 and microondas road 7, 7.2 km NE Coscomatepec, 9.7 km N El Encino, bromeliads, XII.19.1978, G. E. and K. E. Ball (UASM); Fortín de las Flores (UASM); 16.7 km SW Huatusco (UASM); Jalapa (USNM); 4.8 & 10.0 km NW Jalapa (UASM); 1 female, 3 km S Jalapa, V.25–30.1991, B. Ratcliffe, J. S. Ashe, M. Jameson (SEMC); 2 specimens, 35 km. E. Jilotepec, bromeliads, XII.17.1978, G. E. and K. E. Ball (UASM); Lago de Catemaco (UASM); Minatitlán (UASM); 1 ex., Orizaba, VII.27.1960 (MCPM); 8.4 km E Orizaba (UASM); Presidio (USNM); Río Blanco; San Andres Tuxtla (USNM). **COSTA RICA:** 3 specimens, “Costa Rica” (CMNH). **EL SALVADOR. La Libertad:** 4 specimens, Boqueron, nr. Santa Tecla (CNCI, UASM). **Santa Ana:** 3 specimens, 6 km W Hiway CA1, above Lago de Coatapeque, 853 m, VI.1 (USNM); Cerro Verde (USNM). **San Salvador:** San Salvador (BMNH). **GUATEMALA. Alta Verapaz:** 7 specimens, Panzos (MCZC). **Baja Verapaz:** 2 males, 3 females, 8 km S Purulhá, 1660 m, V.19.1991, R. S. Anderson (CMNC); 21 males, 11 females, 8 km S Purulhá, tropical montane forest, 1660 m, V.19–27.1991, G. E. & K. E. Ball & D. Shpeley (UASM); 1 male, 1 female, same, VI.4.1993, H. & A. Howden (UASM); 1 specimen, 32 km S Rabinal, U–V light (USNM); 3 specimens, San Geronimo (MCZC). **Chichicastenango:** 1 specimen, El Naranjo (USNM). **Chimaltenango:** 3 specimens, S. P. Yepocapa (FMNH); 1 specimen, Municipio Yepocapa, Finca Recreo (FMNH). **Huehuetenango:** 1 specimen, La Mesilla (USNM). **Izabal:** 1 female, Cerro San Gil, 8 km N. Las Escobas, V.11.1993, H. & A. Howden (UASM). **Zacapa:** 3 males, 3 females, 3.5 km SE La Union, cloud forest, 1500 m, VI.4.1991, R. S. Anderson (CMNC); 3 males, 2 females, same locality, VI.23.1993, R. Brooks, J. S. Ashe, #084 (SEMC); 1 male, 3 km S La Union, 1400 m, VI.15.1994, H. & A. Howden (UASM); 8 males, 5 females, Sierra del Espíritu Santo, 9 km SE La Union, tropical montane forest, U–V light, 1400–1500 m, G. E. & K. E. Ball & D. Shpeley (UASM). **HONDURAS. Federico Morazán:** 6 males, 3 females, Cerro Uyuca, 30 km E Tegucigalpa, U–V light, 1800 m, V.19–VI.6.1994, H. & A. Howden (UASM); 1 specimen, Zamarano, 777–793 m (UMMZ). **Olancho:** 3 males, Parque Nacional La Muralla, MV + UV light, V.24–VI.1.1995, R. H. Turnbow (RHTC). **Paraiso:** 1 female, 19.4 km SE Zamarano and 9.4 km SE Galera, 1460 m, 13°24'N, 86°55'W, “Los Lavanderos”, ex treefall litter, VI.11.1994, J. S. Ashe and R. Brooks #075 (SEMC). **NICARAGUA. Matagalpa:** Matagalpa (FSCA). **VENEZUELA. Aragua:** 2 specimens, Rancho Grande, V.15.1973, G. Ekis (USNM).

Onypterygia tricolor Dejean

(Fig. 72; 78; 93A, B; 94A, B; 98; 105; 109)

Onypterygia tricolor Dejean, 1831:349. Lectotype (Here designated), male labelled: “Orizaba” [green paper]; “tricolor Chevrolat in Mexico” [green paper]; “Chevrolat” [green paper]; “Ex Musaeo/

Chaudoir" [red print] (MNHP). Chevrolat, 1835:157. Chaudoir, 1837:12. Castelnau, 1840:42. Bates, 1882:131. Heyne and Taschenberg, 1908:25 (see Heyne, 1895).

Onychopterygia tricolor; Gemminger and Harold, 1868:384. Chaudoir, 1878:275.

Onychopterygia tricolor v. *dimidiata* Chevrolat, 1835:157. Type material: not seen; types not fixed. There may be suitable specimens in OXUM, but validation of this name was unintentional. Synonymized by Csiki, 1931:744.

Onychopterygia apicalis Chaudoir, 1837:12. Lectotype (here designated) male, labelled "var. apicalis Chaud." and "Ex Musaeo Chaudoir" [red print] (MNHP). Bates, 1882:131.

Onychopterygia apicalis; Gemminger and Harold, 1868:384. Chaudoir, 1878:275. New synonymy.

Names and Type Material

Possible type material of *O. tricolor* seems restricted to three specimens in the Oberthür–Chaudoir collection (MNHP), each with green Dejean labels. Since Dejean indicated in the original description that the specimen was received from Chevrolat, the male specimen labelled "Höpfner" is rejected. Of the other two specimens, one has a determination label, and is selected here as lectotype.

Chevrolat (1835), after a brief Latin description of *O. tricolor*, wrote: "Var. β Viridis, elytris rubris cum tertia parte apicale coeruleo-violaceis. *Callichroa dimidiata*, Hoepfner (inedita)." (This combination of name and author, being unpublished previously, has no status nomenclaturally.) Following a description and discussion of *O. tricolor* in French, he wrote a similar note in French for *Callichroa dimidiata*. These excellent descriptive statements comprise the earliest validation of the name *O. dimidiata*, albeit unintentional. Thus, this name cannot be attributed to Heyne and Taschenberg (1908; see Heyne, 1895), as done by Csiki (1931) and Blackwelder (1944).

The name *O. apicalis* was based on the western color form, with the dark apical coloration reduced in extent. Only one specimen in Chaudoir's material seems eligible as type, but he did not so state in the original description. Thus, the specimen labelled "var. apicalis Chaud." is selected as lectotype. This label implies an afterthought, since originally, Chaudoir described *O. apicalis* as a distinct species. Chaudoir (1878) considered as synonyms the names *O. dimidiata* and *O. apicalis*.

Type Localities

The type area of nominotypical *O. tricolor* is Mexico, and the type locality is restricted here to Orizaba, Veracruz, Mexico.

The type area of *O. tricolor dimidiata* is "environs de Mexico."

The type area of *O. tricolor apicalis* is Mexico, and the type locality is restricted here to 8.7 km east of Cuernavaca, state of Morelos.

Diagnostic Combination

With character states of the *O. fulgens* group restricted as follows. Elytra bicolored, banded, rufotestaceous basally, and violaceous black apically. Also, pronotum with a single pair of setae (posterolaterals), elytra posteriorly each bidentulate, and female sternum VII posteriorly with more than two pairs of marginal setae.

Description

With diagnostic combination of *O. tricolor* and the following.

Measurements and Proportions.—TL intermediate to large (11.5–14.5 mm), WP/WH low (1.32), LP/WP intermediate (0.78), WP/WPb low (1.18), LE/WE high (1.85).

Color.—Head bright green. Antennae with basal antennomeres partially metallic; apical antennomeres piceous to black. Palpi piceous. Pronotum bright green. Femora metallic, partially black; tibiae and tarsi piceous-black.

Microsculpture, Mesh Pattern.—Head, microlines partially effaced, isodiametric; pronotum, with microlines effaced, surface smooth; elytra, isodiametric.

Chaetotaxy.—Elytron, discal setae three; dorsoapical portion of hind femur without setae; abdominal sterna IV–VI one pair of setae each; abdominal sternum VII, marginal setae—male, two or more pairs; female, three or more pairs.

Head.—Genae smooth. Eyes prominent, convexity marked.

Prothorax.—Pronotum (Fig. 72). Anterior bead complete; lateral beads absent. Posterolateral impressions impunctate, or sparsely punctate; angles broadly rounded. Lateral margins not sinuate. Posterolateral pair of setigerous punctures at posterolateral angles, in contact with lateral margins.

Pterothorax.—Mesepisternum partially punctate. Metepisternum elongate.

Elytra.—Surface smooth. Elytron, humerus broadly rounded; lateral margin narrowly rounded. Apex denticulate; sutural apex denticulate. Interneurs 2–6 continuous, shallow, impunctate. Discal and umbilical punctures not foveate.

Hind Wings.—(Fig. 78) Macropterous.

Legs.—Tarsomeres 1–3 of middle and hind tarsi sulcate. Fore tarsomere 4, inner lobe longer than basal portion; hind tarsomere 4, outer lobe shorter than basal portion.

Male Genitalia.—Median lobe in dorsal aspect (Fig. 93A, 94A) with apical portion very short; apex acute, narrowly to moderately broadly rounded; in left lateral aspect (Fig. 93B, 94B) apical portion narrow, apex acute. Internal sac (Fig. 98) markedly elongate; basal and preapical lobes absent; armature about 17 short, broad spinose sclerites, in two rows—one row extended prebasally to preapically, mainly ventral, one row mainly dorsal; without basal spinose sclerites.

Ovipositor.—(Fig. 105) Stylomere 2 form 3.

Variation

The name *O. dimidiata* represents a distinctive color phase of *O. tricolor* in western and central Mexico (pale morph, Fig. 109), with specimens from Sonora and Chihuahua to the southern end of the Sierra Madre del Sur in Oaxaca on the Pacific Versant tending to have about the basal 60% of the elytron pale with the contrast abrupt. Specimens from eastern and southern Mexico and Central America (nominotypical *O. tricolor*, the dark morph, Fig. 109) tend to have only about the basal 40% of the elytron pale, with the color demarcation gradual. However, some specimens from central Mexico (Tenancingo, in the Transvolcanic Sierra) and in the Sierra Madre del Sur (Cacalutla, Marquelia) are intermediate. Furthermore, there are no differences in other features (such as male genitalia) that correlate with the color differences.

We use the epithet “*dimidiata*” as an informal designation for the paler western Mexican color form. The name is available for formal use and is senior to the epithet *apicalis*.

Habitat

Adults of this species are encountered in vegetation formations ranging from deciduous thorn forest to pine–oak, and in altitude extending from near sea level to about 2300 m. Many specimens were taken at UV light traps at night, most of them from May to October. Although adults are found in bromeliads from December to April, the species is a much less conspicuous part of the dry season bromeliad fauna than are some related species, notably *O. fulgens*.

Geographical Distribution

The range of this species extends from Venezuela northward in western Mexico on the western slopes of the Sierra Madre Occidental to southern Sonora and Chihuahua, and in eastern Mexico along the Atlantic flanks of the Sierra Madre Oriental, to southern Tamaulipas (Fig. 109).

Chorological Affinities

The widest-ranging species of the genus, the range of this species overlaps those of virtually every other species of *Onypterygia*. This is true also of the species to which *O. tricolor* is most closely related, *O. hoepfneri* and *O. sallei*.

Material Examined

About 1400 specimens of *O. tricolor* were seen by us, from the following localities.

MEXICO. Chiapas: 1 male, 1 female, 2 km S Chicosen, road to Mirador, VI.18.1989, H. F. Howden (UASM); 1 male, Cinco Cerros, 860 m, V.31.1990, H. & A. Howden (UASM); 4 specimens, 50–52 km SE Comitán, U-V light (TAMU, UASM); 1 male, 1 female, El Chorreadero, 8 km E Chiapa de Corzo, V.17.1989, H. F. Howden (UASM); Escopetazo, jct. Hwy. 190 & 195; 1 male, 7.4 km N Frontera Comalapa, U-V light, VI.17.1966, Ball and Whitehead (UASM); 1 female, 32.2–40.2 km N Huixtla, VI.30.1969, H. J. Teskey (CNCI); 1 male, Jaltenango, El Triunfo, V.12.1985, H. Velasco (UNAM); 1 male, 3.2 km W Lazaro Cardeñas, VI.26.1969, J. M. Campbell (CNCI); 1 specimen, 1 km E Navenchauc, bromeliads, I.13 (UASM); 1 male, Parque El Aguacero, 16 km W Ocozocoautla, VI.9.1989, H. F. Howden (UASM); 1 female, same, VI.24.1989 (UASM); 1 specimen, 13 km E Rizo de Oro (UASM); 1 male, Ruinas Chincultic, 1500 m, VI.30.1990, B. D. Gill (CMNC); 1 male, 2 females, San Cristobal de las Casas VI.7, H. F. Howden (CNCI); 1 male, 32.2 km W San Cristóbal de las Casas, V.20.1969, J. M. Campbell (CNCI); 11.3 km E Simojovel (CISC); 1 male, 13 km S Simojovel, jct. Hwys. 190 & 195, VI.10.1969, J. M. Campbell (CNCI); 2 females, same, VI.6.1969 (CNCI); 1 male, 2 females, 27.4 km SE Teopisca, VI.3–4, H. F. Howden (CNCI); 1 male, 1 female, 125.5 km W Tuxtla Gutiérrez, VII.27 (CISC). **Chihuahua:** 2 specimens, 6.4 km N. Las Chinacas (nr. Sonora border), 1494 m, VII.9–10.1989, S. McCleve (UASM). **Colima:** 1 female, 42 km SW Colima (MCPM); 14.5–16.0 km NE Comala (TAMU); 30 males, 26 females, Tecuiztitlan, VII.26.1967, Ball, T. L. Erwin and R. E. Leech (UASM); 10 males, 2 females, Volcan de Colima (USNM). **Guerrero:** 1 male, Apipilulco (USNM); 1 female, 5.3 km N. rd. to Buenavista de Cuellar (USNM); nr. Cacahuamilpa (TAMU); 9.7 km SE Cacalutla (TAMU); 1 male, Chilpancingo, VII.23 (CISC); 1 male, 29 km N. Chilpancingo, VII.18 (UCDC); 1 female, Km 95, Coyuca–Zihuatanejo, VII.25.1985, F. Arias & Y. Barba (UNAM); 1 female, Ixcuinatoyac, IX.10 (USNM); 6.0 km E Marquelia (TAMU); 3 specimens, 8 km S Mazatlán, Hwy 95, 1130 m, VI.29.1992, C. Bellamy (CMNH); 1 male, 1 female, 12.6 km S Mazatlán, VI.28 (USNM); 2 specimens, 2.5 km S Milpillás, Hwy. 95, VII.17.1992, C. Bellamy (CMNH); 4 specimens, 7 km N. Milpillás, 600 m, VI.30.1982, J. E. Rawlins (CMNH); 1 male, 2.5 km S Taxco, 1800 m, IX.19.1989, R. Turnbow (RHTC). **Hidalgo:** 2 males, 1 female, El Barrio, VI.18 (UASM); 1 male, 38.3 km NE Jacala, XI.13.1965, Ball and Whitehead (UASM). **Jalisco:** 2 males, Ajijic nr. Atenquique, VII.16–18 (USNM); 25.7 & 32.2 km SW & 16 km N. Autlán (CDAE, CASC, TAMU); 1 male, Chapala, VII.8 (CISC); 1 male, 9.7 km W Chapala, VI.20.1963, J. Doyen (CNCI); 5 specimens, 15 km W El Texquequite, 1046 m, VI.30.1977, J. E. Rawlins (CMNH); 1 male, 3 females, Guadalajara, VII.17–20.1967, Ball, T. L. Erwin, and R. E. Leech (UASM); 27 km N Guadalajara (TAMU); 1 male, 16.1 km E Ixtlán del Río, VIII.10 (MCPM); 1 specimen, Jamay (TAMU); 1 male, 33.2 km NW Magdalena, VII.30 (CISC); 2 specimens, 25.7 km SW Mazamitla (CDAE); 2 specimens, 5 km SE Plan de Barrancas (UCDC); 1 specimen, 19.3 km W Poncitlán (TAMU); 1 specimen, 34.9 km S Puerto Vallarta (CDAE); 1 specimen, San Sebastián, Sierra Madeiro, Sierra Madeiro Mts (CASC); 1 specimen, 52.3 km S Tecalitlán (UASM); 1 male, 4 females, 8.8 km NE Tecolotlán (CDAE); 6 males, 8 females, Volcán Tequila, 10–14 km SSW Tequila, XI.8.1974, D. E. & J. A. Breedlove (CASC). **México:** 2 males, 3 females, Temascaltepec, (CASC); 6.4 km S Tenancingo, bromeliads, IV.22.1966 (UASM). **Michoacán:** 2 males, 87.1 km W Apatzingan, road to Dos Aguas (UASM); 2 females, Atzimba Nat. Park, III.25 (UCDC, USNM); 1 female, 17.7 km S Tzitzio, on Huetamo rd., 19°20'N, 100°50'W, VII.10.1947, T. H. Hubbell (UMMZ); 1 specimen, 24 km E Zamora, VIII.14 (UASM). **Morelos:** 2 specimens, Cañon de Lobos, Km 19 E Cuernavaca, 1120–1375 m, VII.3.1992, C. Bellamy (CMNH); 1 male, 3 females, Cuernavaca, 1676 m, H. E. Evans (CUIC); 11 males, 9 females, 6.4 km E Cuernavaca, 1829 m, VI.6–23.1959, H. E. & M. A. Evans (CUIC); 11 males, 9 females, 8.4 km E Cuernavaca, U-V light, VI.23–30. 1966, Ball and Whitehead (UASM); 1 female, 11.3 km E Cuernavaca, VII.15.1969, J. M. Campbell, D. E. Bright (CNCI); 5 males, 1 female, Huejintlán, VII.21, VIII.22 (UASM); 2 females, Puente de Ixtla (UASM); 1 male, 1 female, near Tlalpa (UASM); 1 male, Tequesquitengo, VII.15 (UASM); Xochicalco; Yautepec (UCDC). **Nayarit:** 3 females, Ahuacatlán, nr. Compostela, VII.18–22 (UASM); 12 males, 16 females, 11 km E Compostela, Rte. 68D, 1250 m, U-V light, VII.23 (UASM); 1 male, 1 female, El Pichón, VI.25 (CISC); 6 males, 2 females, Jesus Maria, VII.6–27 (CISC); 16 males, 16 females, La Mesa de Nayar, VII.19–21 (CISC); 2 specimens, 57.9 km SW Las Piedras (UASM); San Blas (FSCA, USNM); 4 males, 5 females, San Juan Peyotán, VIII.2 (CISC); 6 males, 3 females, Tepic, VIII.7 (CISC); 4 males, 3 females, Tepic (UASM); 4 specimens, 23 km S Tepic, 1070 m, VII.17.1977, J. E. Rawlins (CMNH); 1 specimen, 29.0 km S Tepic (TAMU); 2 females, Volcán Ceboruco, 8–12 km N. Jala, X.4.1990, J. E. Wappes (JEW); 1 male, same, 4.9 km S Jala, X.7.1992, R. Turnbow (RHTC). **Oaxaca:** 3 males, 3 females, Juchatengo VII.19.1966, U-V Light, Ball and Whitehead (UASM); 82.5 km S Juchatengo (UASM); 2 males, La Ventosa, 115.8 km E Oaxaca, J. Doyen (CISC, CUIC); 4 specimens, 6 km E

Pinatapa near river, 180 m, VIII.16.1986, J. Rawlins, R. Davidson (CMNH); 1 female, 10 km E Tapatepec (UASM); 8.0 km W Tehuantepec; 1 female, 71 km W Tehuantepec, VII.21 (CISC); 2 males, 1 female, 9.7 km S Valle Nacional, V.18.1971, D. E. Bright (CNCI). **Puebla:** 1 female, near Tepexco, IX.5.1965, Ball and Whitehead (UASM). **San Luis Potosí:** 1 male, El Naranjo, VI.29.1966, Ball and Whitehead (UASM); 1 specimen, El Salto (FSCA); 1 male, 1 female, El Salto falls, 12 km NW El Naranjo, 400 m, U-V light, VII.2.1990, J. S. Ashe, K. J. Ahn, R. Leschen (SEMC); 1 male, same, VII.4.1990, R. L. Minckley (SEMC); 2 specimens, Puerto Verde, 64 km W Ciudad Valles (TAMU); 3 specimens, Tamán, ca. 16 km SW Tamazunchale (UASM); 1 male, Tamazunchale, VII.28 (UASM); 1 male, 29 km SW Tamazunchale VIII.2 (CISC); 2 females, Xilitla VII.21 (UASM); 1 specimen, 3.2 km E Xilitla (TAMU); 1 specimen, Hwy 70, km 82, microondas rd. jct (TAMU). **Sinaloa:** 61 km NE Concordia (CDAE, TAMU); 3 males, 4 females, Culiacán, VII.21.1959, H. E. Evans (CUIC); 9.7 km S Culiacán (CISC); 1 female, 16 km. N. Mazatlán, VIII.7 (MCPM); 1 female, Microondas El Indio, Hwy. 15, 370 m, Sinaloan thorn forest, U-V light, 93.30, VII.18.1993, S. McCleve, G. E. & K. E. Ball (UASM); 2 males, Pánuco, intercepted with orchids (USNM); 1 male, Venedillo, VI.6 (CASC); 34 & 43 km E Villa Union, VII.25–26 (CISC). **Sonora:** 1 male, 91 km N Culican, VIII.28 (UCDC); 1 female, 5.1 km NW Huicoche, 1577 m, U-V light, VII.11–13.1989, S. McCleve (UASM). **Tamaulipas:** 1 specimen, 8.0 km SSE Gómez Farías (TAMU). **Veracruz:** 1 female, Acayucan, X.23 (UASM); 19.3 km NW Amate (TAMU); 13–16 km NE & 34 km S Catemaco (CISC); 10 specimens, Córdoba (CISC); 115 specimens, Cotaxtla (CISC); 19 specimens, 7.2 km NE Coscomatepec, bromeliads, XII.19.1978, G. E. and K. E. Ball (UASM); 1 female, Cuitlahuac (USNM); 6 males, 4 females, Dos Amates, VII.16–17.1969, D. E. Bright, J. M. Campbell (CNCI); 1 male, Fortín de las Flores, VI.29.1964, A. G. Raske (CNCI); 0–3.2 km W Fortín de las Flores, bromeliads, III.7 (CISC); 8 km N, 11.3 km NE, & 32.2 km NW Huatusco (UASM); Jalapa (UASM, USNM); 1 female, 2.5 km S Jalapa, 1370 m, light, V.28.1991, J. S. Ashe (SEMC); 5 males, 1 female, 10 km NW Jalapa, bromeliads, IV.8.1966, Ball and Whitehead (UASM); 1 female, La Tinaja, VII.27 (UASM); Lake Catemaco (FSCA, TAMU); 1 male, Nacimiento de Río Atojal, VII.13.1966, Ball and Whitehead (UASM); Orizaba (CASC, MCPM); 1 female, 4.8 km NE Orizaba, 1219 m, IX.3.1959, I. J. Cantrall, T. J. Cohn (UMMZ); 1 male, Presidio, VII.30 (USNM); 1 female, Río Blanco, IX.13 (UASM); 40 specimens, San Andres Tuxtla, IV.27 (USNM); 1 female, 11.3 km N. Santiago Tuxtla, VII.8.1963, J. Doyen (CNCI); 9 males, 1 female, 4 km W, 10.6 km E Sontecomapan, VI, VII, IX (UASM); 3 males, 9.7 km S Sontecomapan, Clark & Cave (AUEM); 2 females, 8 km S Sontecomapan, IX.7.1982, Clark & Cave (AUEM); 1 female, Tuxpango–Orizaba, VIII.13 (USNM); Veracruz. **BELIZE, Cayo District:** 1 specimen, Chiquibul River, VI.21–23.1985, Ellen Censky (CMNH). **COSTA RICA. Alajuela:** 1 specimen, Alajuela (USNM). **Guanacaste:** 3 specimens, Bebedero, VI.13, VII.4 (USNM); 1 specimen, Hacienda Palo Verde (USNM); 1 specimen, La Pacifica, nr. Cañas (JEWIC); 1 female, Maritza Biological Strn., Parque Nacional Guanacaste, V.21.1993, D. Brzoska (SEMC); 3 specimens, Santa Rosa National Park (USNM). **Puntarenas:** 1 specimen, 6 km S Santa Elena (JEWIC); 1 male, 2 females, Monteverde area, VI.4–6.1980, J. E. Wappes (UASM); 1 male, Monteverde, U-V light, V.7–12.1989, E. Fuller (UASM); 1 female, same, V.25 & 28.1979; 5 males, 3 females, same, U-V light, V.10.1989, J. S. Ashe, R. Brooks, R. Leschen (SEMC); 1 male, 4 females, same, 1550 m, V.24.1989; 1 female, same, flight intercept trap, 1570 m, V.14.1989; 1 male, Monteverde, Cerro Amigas, ex leaf litter at base of tree, 1785 m, V.22.1989; 1 male, 2 females, Monteverde, Pension Quetzal, VI.5.1992, F. Andrews & A. Gilbert (CDAE). **San José:** 4 specimens, Atenas (MCZC, USNM); 3 specimens, San José (USNM). **EL SALVADOR.** 1 male, Cerro Verde, 2000 m, V.1.1971, H. F. Howden (UASM); 1 specimen, Landaverde (FSCA). **La Libertad:** 76 specimens, Boquerón (CNCI); 2 specimens, Los Chorros (FSCA); Quetzaltepeque (UCDC); 2 specimens, 4.0 km and 4.8 km S Quetzaltepeque (USNM); 3 specimens, Santa Tecla (FSCA, USNM). **La Union:** 4 specimens La Union (USNM). **San Salvador:** 2 specimens, San Salvador, V.22 (USNM). **Santa Ana:** 2 specimens, 6 km W Hwy. CA 1, above Lago de Coatepeque, 853 m, VI.1 (USNM); Montecristo, 2300 m (FSCA, USNM); 4 males, 2 females, Monte Cristo, 2300 m, V.9.1971, H. F. Howden, S. B. Peck (UASM). **GUATEMALA. Alta Verapaz:** 1 specimen, 22.2 km W La Tinta. U-V light (USNM); 1 specimen, Panzós (MCZC). **Chimaltenango:** 2 specimens, S. P. Yepocapa (USNM). **Escuintla:** 3 specimens, Zapote (FMNH). **San Marcos:** 1 specimen, 17.3 km SE Talisman, Río Cabús (USNM). **Suchitepequez:** 1 male, Finca El Ciprés, VI (CASC). **Zacapa:** 1 female, 3 km E La Union, VI.6.1991, H. F. & A. Howden (UASM); 1 female, Sierra del Espíritu Santo, 3 km SE Limon, tropical montane forest, beating vegetation, 1400–1500 m, VI.6.1991, D. Shpeley, G. E. & K. E. Ball (UASM); 2 females, same, but at U-V light. **HONDURAS. Copán:** 1 male, 1 female, 19 km SW Sta. Rosa de Copán, X.8.1993, R. Turnbow (RHTC). **El Paraíso:** 17 km NW Jacaleapa, X.12.1993, R. Turnbow (RHTC); 1 male, Cerro Montserrat, 7 km SW Yuscarán, 1800 m, V.21.1994, H. & A. Howden (UASM). **Federico Morazán:** 1 male, 3 females, Cerro Yyuca, 30 km E Tegucigalpa, 1800 m, V.16 & 19.1994, H. F. & A. Howden (UASM); 2 specimens, nr. Tegucigalpa (FSCA); 4 specimens, Zamorano (UMMZ). **Olancho:** Parque Nacional La Muralla, V.24–

VI.1.1995, R. H. Turnbow (RHTC). **NICARAGUA. Managua:** Managua. **Rivas:** 1 specimen, Río Canas Gordas, km 133, bet. La Virgena & Sapoá (FSCA); 1 female, Leon, VI.1989, J. M. Maes (UNAN); 1 male, Grenada v. Mombacho, VII.1989, F. Reinholdt (UNAN). **PANAMA.** 2 specimens, Santa María El Real (MCZC). **Coclé:** 1 specimen, El Valle (USNM). **Panama:** 1 specimen, Cerro Campana, Hespeneheide (USNM); 1 female, Cerro Azul & Cerro Jefe at standing lights, V.11.1991, R. H. Turnbow (RHTC); 1 specimen, 80 km E Chepo (USNM). **VENEZUELA. Aragua:** 4 males, 1 female, Rancho Grande, V.15.1973, G. Ekis (USNM).

Onypterygia hoepfneri Dejean

(Fig. 1; 3; 9; 73; 79; 95A, B; 99; 106; 110)

Onypterygia hoepfneri Dejean, 1831:347. Lectotype (here designated) male, labelled: "Höpfneri in Mexico" [green paper]; "D. Höpfner" [green paper]; "Ex Musaeo/Chaudoir" [red print]. Castelnau, 1840:42. Bates, 1882:130. Heyne, 1895:25.

Onychopterygia hoepfneri; Gemminger and Harold, 1868:384. Chaudoir, 1878:275.

Type Locality

Type area Mexico, type locality here restricted to 8.7 km east of Cuernavaca, state of Morelos.

Diagnostic Combination

With character states of the *O. fulgens* species group, restricted as follows. Large in size, with submetallic to metallic green or blue fore body, and markedly alutaceous maroon elytra, adults of *O. hoepfneri* are distinguished from those of the closely related, allopatric *O. sallei* by having inconspicuous preapical elytral calli, and less distinctly punctate posterolateral pronotal impressions.

Description

With diagnostic combination of *O. hoepfneri* and the following.

Habitus.—As in Figure 1.

Measurements and Proportions.—TL intermediate to large (13.0–17.5 mm), WP/WH low (1.24), LP/WP intermediate (0.82), WP/WPb low (1.16), LE/WE intermediate (1.73).

Color.—Head bright green. Antennae with basal antennomeres partially metallic; apical antennomeres piceous-black. Palpi piceous. Pronotum bright green. Elytra with disc concolorous, maroon. Femora metallic, partially black; tibiae and tarsi piceous-black.

Microsculpture, Mesh Pattern.—Head, isodiametric; pronotum, microlines effaced, surface smooth; elytra (Fig. 3), isodiametric.

Chaetotaxy.—Pronotum, lateral setae one pair; elytron, discal setae three; dorsoapical portion of hind femur without setae; abdominal sterna IV–VI one pair of setae each; abdominal sternum VII, marginal setae male, two or more pairs; female, three or more pairs.

Head.—Genae smooth, not rugose. Eyes prominent, convexity marked.

Prothorax.—Pronotum (Fig. 73). Anterior bead complete; lateral beads absent anteriorly, evident posteriorly. Posterolateral impressions impunctate, or sparsely punctate; angles broadly rounded. Lateral margins not sinuate. Posterolateral pair of setigerous punctures at posterolateral angles, on bead.

Pterothorax.—Mesepisternum partially punctate. Metepisternum elongate.

Elytra.—Surface smooth. Elytron, humerus broadly rounded; lateral margin narrowly rounded. Apex angulate; sutural apex rounded. Interneurs 2–6 discontinuous, series of small punctures. Discal and umbilical setigerous punctures not foveate.

Hind Wings.—(Fig. 79) Macropterous.

Legs.—Tarsomeres 1–3 of mid- and hind tarsi sulcate. Fore tarsomere 4, inner lobe longer than basal portion; hind tarsomere 4, outer lobe shorter than basal portion.

Male Genitalia.—(Fig. 95A, B; 99) Median lobe in dorsal aspect with apical portion short; apex broadly rounded; in left lateral aspect (Fig. 95B), apical portion slender, apex acute. Internal sac (Fig. 99) markedly elongate; basal and preapical lobes absent; armature of 28 spinose sclerites, as follows—three in basal group (one dorsal, one left ventral, and one left ventral), remaining in two rows (one dorsal, one ventral), extended from prebasal area to apex.

Ovipositor.—(Fig. 106) Stylocere 2 form 3.

Variation

Although we consider *O. sallei* from Veracruz distinct from *O. hoepfneri* to the south and west, we are not satisfied fully that these are distinct species. The two taxa are closely related and may prove to be linked by intermediates (as has been found for *O. thoreyi* and *O. fulgens*, see above), and in this discussion, we consider them together. Both forms were recorded by Bates (1882:130) from Juquila, but the record of *O. sallei* is based on a specimen of *O. hoepfneri*, and it seems that *O. sallei* lives only in central Veracruz.

Available samples of *O. hoepfneri* and *O. sallei* form four geographical clusters of more or less recognizable forms: central Mexico (Guerrero, Jalisco, México, Michoacán, and Morelos), the Sierra Madre del Sur of Oaxaca, Chiapas-Honduras, and central Veracruz (*O. sallei*). Character states of the Oaxaca specimens are intermediate between those from Chiapas and central Mexico.

The Veracruz morph seems both disjunctive and distinctive, but nonetheless more similar to *O. hoepfneri* from Chiapas than from Oaxaca or central Mexico. Most readily observed variables seem to form clines from central and western Mexico, south to Chiapas, and north in the east to central Veracruz. The most distinctly marked of these are elytral color (more greenish toward Veracruz), numbers of ambulatory setae on abdominal sterna IV-VI (increasing toward Veracruz), number of spinose sclerites on the internal sac (decreasing toward Veracruz), width of lateral margins of pronotum (broadest in Veracruz), color of fore body (most markedly metallic in Veracruz), and form of elytral apex (most markedly produced and angulate in Veracruz).

However, we consider the allopatric *O. sallei* distinct from *O. hoepfneri* because its known distribution is disjunctive and available specimens are distinguishable at a glance. *Onypterygia hoepfneri* has much more markedly alutaceous and hence less brilliantly colored elytra than does *O. sallei*. The elytra characteristic of the latter species have rather marked preapical calli, and these are lacking from or inconspicuous in *O. hoepfneri*. In *O. sallei*, the pronotal posterolateral impressions are markedly, densely punctate; in *O. hoepfneri*, these impressions are much more finely and less distinctly punctate. Another discontinuity is in size: the Veracruz specimens smaller, and those from Chiapas larger.

No evident geographical variation was found in numbers of posterior marginal setae of abdominal sternum VII. In 40 males of *O. hoepfneri* and three of *O. sallei*, the number of setae ranged from 22 to 33, sample means 26.3 to 27.2.

This lack of differentiation contrasts with variation observed in total numbers of paramedian ambulatory setae on abdominal sterna IV-VI: female sample means 6.0, 6.7, 9.3, and 12.0, and male means 6.0, 6.0, 7.2, and 8.0, in central México, Oaxaca, Chiapas, and Veracruz, respectively.

Habitat

Adults of this species have been collected in bromeliads (January through May), on foliage (August), and at UV light traps (June, July), at middle elevations from 1000 to about 2100 m altitude, in tropical deciduous thorn forests, oak forests, pine-oak forests, and montane rain forests.

Geographical Distribution

The range of this species extends from El Salvador and Honduras northward to Jalisco Sinaloa in the Sierra Madre Occidental (Fig. 110). It is not known from Veracruz.

Chorological Affinities

As noted above, this species and its putative adelphotaxon are allopatric. More generally, the range of *O. hoepfneri* overlaps the ranges of most of the other species of *Onypterygia*.

Phylogenetic Relationships

This species and *O. sallei* are postulated to be adelphotaxa. For details see the "Variation" section above.

Material Examined

We have seen about 175 specimens of *O. hoepfneri* from the following localities.

MEXICO. Chiapas: 1 female, 65 km E Bochil, IX.13.1981, Clark & Coe (AUEM); 1 female, NW slope Baul, W. Rizo de Oro, 1768 m, X.12.1979, D. E. & J. A. Breedlove (CASC); 1 male, Cerro Bola, N Cerro Tres Picos, 1500–2100 m, V.5.1972, D. Breedlove (CASC); 2 females, nr. Chiapa de Corzo, jct. Hwy. 190 & 195, VI.24 (USNM); 3 males, 2 females, 47.8 km N. Huixtla, 1311 m, in bromeliads, II.26.1966, Ball and Whitehead (UASM); 1 female, Parque Nacional de Laguna de Montebello, Laguna Pojoj, VI.12.1989, H. F. Howden (UASM); 1 male (teneral), same, Dos Lagos, on rd. to Santa Elena, 1219 m, D. E. & J. A. Breedlove (CASC); 1 female, Pueblo Nuevo, 1547 m, in bromeliads, V.25.1966, Ball and Whitehead (UASM); 2 males, 5.0 km S Pueblo Nuevo, 1646 m, in bromeliads, IV.27.1966, Ball and Whitehead (UASM); 1 male, Puerto Cate, IX.9.1981, Clark & Coe (AUEM); 12.7 km S Tapilula, 1463 m, cloud forest, VII.7.1966, Ball and Whitehead (UASM); 17 km W Tuxtla Gutiérrez, 1006 m (FSCA). **Colima:** 3 males, 5 females, vic. El Terrero, Los Sauces rd., km 7–8, X.4.1992, R. H. Turnbow (RHTC). **Guerrero:** Taxco; 1 male, 16 km WSW Xochipala, 1770 m, VI.30.1982, J. E. Rawlins (CMNH). **Jalisco:** 1 female, San Sebastián, Sierra Madeiro (CASC); 52.3 km S Tecalitlán, 1570 m, VIII.4.1967 (UASM). **México:** 1 female, Ixtapan de la Sal, 1768 m, U-V light, VII.12.1966, Ball and Whitehead (UASM); 4 males, 8 females, Ixtapan de la Sal, in bromeliads, III.5 (USNM); 4 males, 4 females, Temascaltepec (CASC); 1 female, same, 1931, G. B. Hinton (UNAM); 2 females, same, II.9.1979, H. Brailovsky (UNAM); 1 specimen, E. Valle de Bravo, Río de Molino, 2300 m, oak–pine forest, in bromeliads, IV.21.1966, Ball and Whitehead (UASM); 2 males, 1 female, nr. Valle de Bravo, VIII.3.1962, G. E. Ball (UASM). **Michoacán:** 4 males, 1 female, 28.2 km E Morelia, 2134 m, I.11 and 20.1966, Ball and Whitehead (UASM). **Morelos:** Cuernavaca, V.11.1959, H. E. Evans (CUIC); 3 males, 3 females, 7 km, & 7.1–8.7 km E Cuernavaca, 1402–1768 m, Ball and Whitehead (UASM). **Nayarit:** 1 female, 23 km S Tepic, 1066.8 m, J. E. Rawlins (CMNH). **Oaxaca:** Juquila (BMNH); 1 female, 55.5 km N. Pochutla, 1433 m, III.19–20.1966, Ball and Whitehead (UASM); 1 female, Portillo del Rayo, X.18.1985, E. Barrera (UNAM); 10 males, 7 females, 30.7 km S Suchixtepec, 1372 m, in bromeliads, III.17.1966, Ball and Whitehead (UASM). **Sinaloa:** 1 male, 7 km NE La Capilla del Taxte, 1250 m, VI.27.1977, J. E. Rawlins (CMNH). **EL SALVADOR. Santa Ana:** 1 female, Monte Cristo, 2300 m, V.9.1971, Howden & Peck (UASM). **GUATEMALA. Alta Verapaz:** Panzós (MCZC). **Baja Verapaz:** 1 male, 5 km E Purulhá, 1530–1650 m, VII.22–24.1977, E. Fisher, P. Sullivan (CASC); 1 female, 8 km S Purulhá, 1660 m, ex under bark, VI.30.1993, J. S. Ashe and R. Brooks, #162 (SEMC); Sabo (MCZC); 2 males, Sabo (USNM). **Chimaltenango:** S. P. Yepocapa, 1463 m (FMNH). **Escuintla:** 1 male, 8 km N. San Vicente Pacaya, 1371 m, V.14.1966, J. M. Campbell (CNCI). **Quetzaltenango:** Cerro Zunil (MCZC); 3 males, 1 female, same (USNM); 1 female, Los Pirineos Santa Maria, 1371.6 m, V.17.1966, J. M. Campbell (CNCI). **Sacatepéquez:** Dueñas (MCZC); 2 males, Dueñas (USNM). **Totonicapán:** Volcán Santa Maria, 1500 m, VI.19 (USNM). **Suchixtepec:** 1 female, 2 km N. Finca Colimas Zunilito, 1828.8 m, V.6.1966, J. M. Campbell (CNCI). **HONDURAS. El Paraíso:** 1 male, Cerro Montserrat, X.3.1993, R. R. Turnbow (RHTC).

Onypterygia sallei Chaudoir

(Fig. 16, 74, 96, 100, 110)

Onypterygia sallei Chaudoir, 1863:255. Lectotype (here designated) male, labelled "Cordova"; "Mexico./Sallé Coll."; "Onychopterygia sallei Chaud. . . Sallé"; "H. W. Bates/Biol. Centr. Amer." (MNHP). Bates, 1882:130.

Onychopterygia sallei; Gemminger and Harold, 1868:384. Chaudoir, 1878:275.

Type Locality

Córdoba, Veracruz, Mexico.

Diagnostic Combination

With character states of the *O. fulgens* species group, restricted as follows. A large-sized member of the *O. fulgens* group, with metallic green fore body and shiny, only slightly alutaceous, coppery-green elytra, *O. sallei* adults are distinguished from those of the closely related *O. hoepfneri* by having conspicuous preapical calli, and much more markedly punctate posterolateral pronotal impressions.

Description

With diagnostic combination of *O. sallei* and the following.

Measurements and Proportions.—TL large (13.5–15.0 mm), WP/WH low (1.31), LP/WP intermediate (0.73), WP/WPb low (1.19), LE/WE intermediate (1.74).

Color.—Head bright green. Antennae with basal antennomeres partially metallic; apical antennomeres piceous to black. Palpi piceous. Pronotum bright green. Elytra with disc concolorous. Femora metallic, partially black; tibiae and tarsi piceous to black.

Microsculpture, Mesh Pattern.—Head, with microlines partially effaced, isodiametric; pronotum, with microlines effaced, surface smooth; elytra, isodiametric.

Chaetotaxy.—Pronotum, lateral setae one pair; elytron, discal setae three; dorsoapical portion of hind femur without setae; abdominal sterna IV–V with one pair each; sternum VI with two pairs; sternum VII, marginal setae male, two or more pairs; female, three or more pairs.

Head.—Genae rugose, lines fine. Eyes prominent, markedly convex.

Prothorax.—Pronotum (Fig. 74). Anterior bead incomplete; lateral beads absent anteriorly, evident posteriorly. Posterolateral impressions densely punctate; angles broadly rounded. Lateral margins not sinuate. Posterolateral pair of setigerous punctures at posterolateral angles, on bead.

Pterothorax.—Mesepisternum partially punctate. Metepisternum elongate.

Elytra.—Surface smooth. Elytron, humerus broadly rounded; lateral margin slightly sinuate medially. Apex angulate; sutural apex rounded. Interneurs 2–6 discontinuous, series of small punctures. Discal and umbilical setigerous punctures not foveate.

Hind Wings.—Macropterous.

Legs.—Tarsomeres 1–3 of mid- and hind tarsi sulcate. Fore tarsomere 4, inner lobe longer than basal portion; hind tarsomere 4, outer lobe shorter than basal portion.

Male Genitalia.—Median lobe in left lateral aspect (Fig. 96) with apical portion broadly triangular, short; apical portion very short; apex acute. Internal sac (Fig. 100), markedly elongate; basal and preapical lobes absent; armature of 16 spinose sclerites, as follows—basal group three (one ventral, two dorsal), and two apical groups of seven and six (ventral and dorsal rows, respectively).

Ovipositor.—(Fig. 16) Stylomere 2 form 3.

Variation

See discussion of this topic for *O. hoepfneri* above.

Habitat

This species occurs in montane rain forests, in middle elevations (between 880 and 1100 m). Five dated specimen records are from April 27–28, at UV light trap; June 21–30; August 16; October 18; and November 25.

Geographical Distribution

This species is known only from below the eastern flanks of Volcán Citlaltepetl (Orizaba), in central Veracruz (Fig. 110).

Material Examined

We have seen 16 specimens of *O. sallei* from the following localities in Mexico.

Veracruz: Córdoba (BMNH, MNHP); 5 km NE Coscomatepec, 1128 m, cloud forest, VI.21.1966, Ball and Whitehead (UASM); 1 female, Fortín de las Flores (UASM); 1 female, same, U-V light, IV.27–28 (FSCA); 3.2 km W Fortín de las Flores, VIII.16 (CISC); Jalapa (BMNH, AMNH); 1 male, same, Instituto de Ecología, 1300 m, ex epiphytes, XI.25.1994 (FFPC); Río Blanco (UNAM).

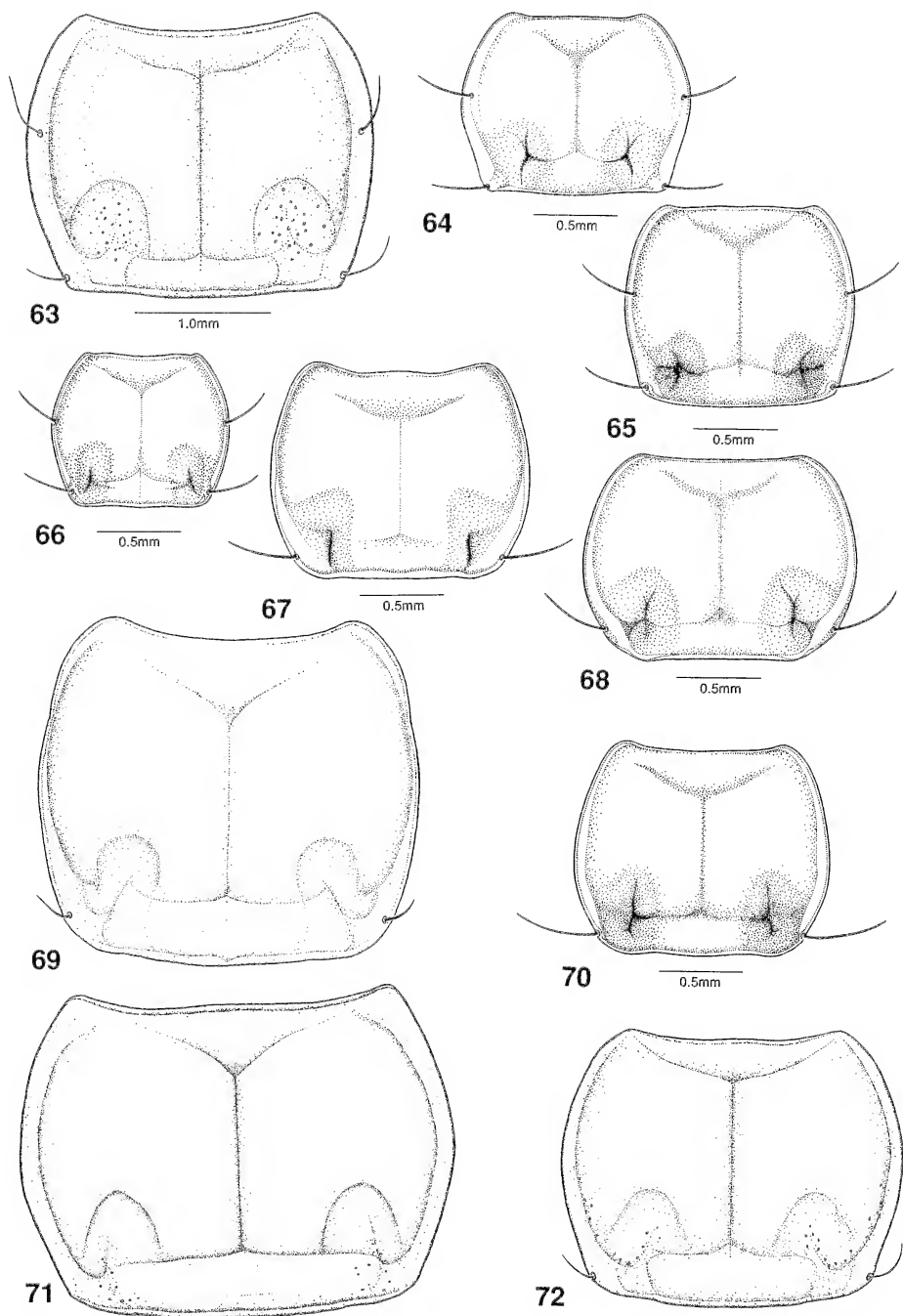


Fig. 63–72.—Line drawings of pronota, dorsal aspect, of species of the *O. fulgens* species group: 63, *O. iris* Chaudoir; 64, *O. championi* Bates; 65, *O. chrysura* Bates; 66, *O. kathleenae*, n. sp.; 67, *O. exeuros*, n. sp.; 68, *O. crabilli*, n. sp.; 69, *O. quadrispinosa* Bates (Guatemala); 70, same (Costa Rica); 71, *O. fulgens* Dejean; 72, *O. tricolor* Dejean.

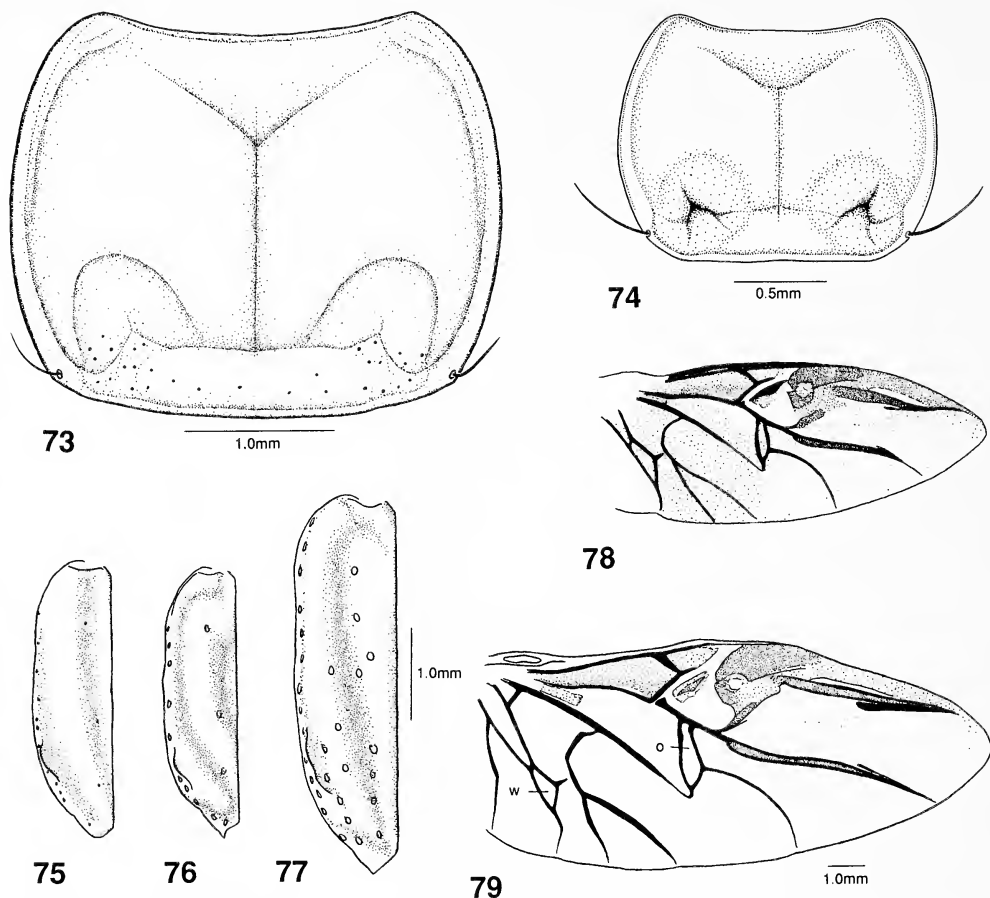


Fig. 73-79.—Line drawings of adult structural features of the *O. fulgens* species group. Fig. 73, 74, pronotum, dorsal aspect, of: 73, *O. hoepfneri* Dejean; 74, *O. sallei* Chaudoir. Fig. 75-77, left elytron dorsal aspect, of: 75, *O. iris* Chaudoir; 76, *O. championi* Bates; 77, *O. polytreta*, n. sp. 78, 79, left hind wing, ventral aspect of: 78, *O. tricolor* Dejean; 79, *O. hoepfneri* Dejean. Legend: o—oblongum cell, w—wedge cell.

ECOLOGICAL ASPECTS AND EVOLUTIONARY CONSIDERATIONS

Ecological Aspects

Data are not adequate for a detailed assessment of this subject. A few generalizations are sought, principally in the label data on specimens, which include limited information about: diel activity patterns, altitude occurrence and distribution, and habitat.

Altitude

Most species of *Onypterygia* are represented between 700 and 2000 m above sea level, with a few taxa known from higher altitudes only, and a few from lower (Table 4). However, the altitudinal ranges of *O. fulgens* and *O. tricolor* are very extensive (from sea level to 2300 m or more), and that of *O. fulgens* covers nearly the entire range of the genus. These latter two species have also the most extensive geographical ranges in *Onypterygia*.

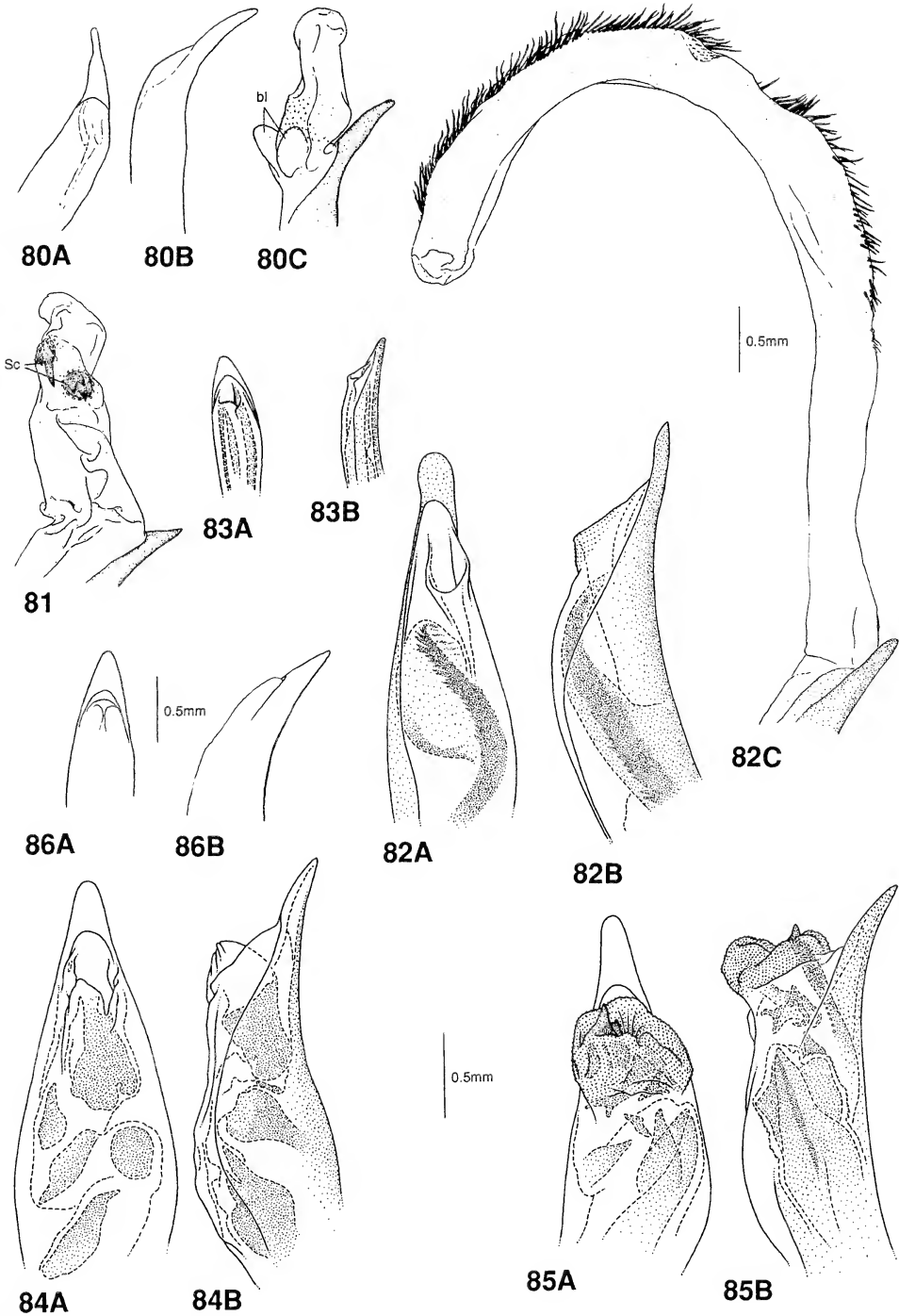


Fig. 80–86.—Line drawings of male genitalia of species of the *O. fulgens* species group: A, B, dorsal and left lateral aspects, respectively; C, left lateral aspect, with internal sac everted. 80, *O. iris* Chau-doir; 81, *O. championi* Bates; 82, *O. chrysura* Bates; 83, *O. kathleenae*, n. sp.; 84, *O. polytreta*, n. sp.; 85, *O. crabilli*, n. sp.; 86, *O. quadrispinosa* Bates. Legend: bl—basal lobes, Sc—spinose sclerites.

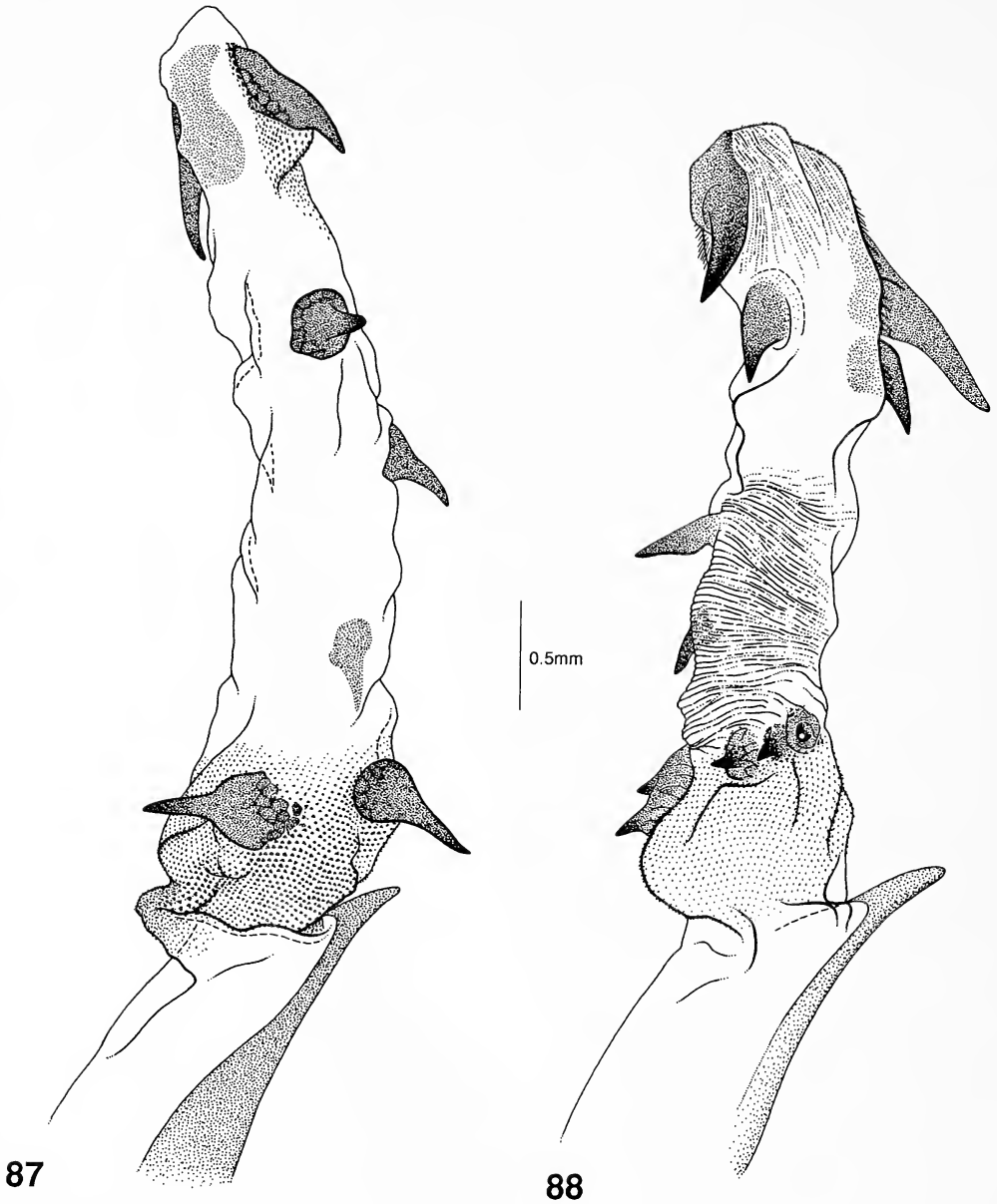


Fig. 87, 88.—Line drawings of median lobes of male genitalia, left lateral aspect, internal sac everted, of the *O. fulgens* species group: 87, *O. polytreta*, n. sp.; 88, *O. crabilli*, n. sp.

The correlated occurrence of two lineages (*wappesi* and *aeneipennis* species groups) at higher altitudes only (1400 m and above) and the brachypterous or wing-dimorphic condition of most of the included species (Table 4) is consistent with Darlington's observations (1971:165–172) based on study of New Guinea Carabidae, that flightlessness is selected for at such altitudes, and that the flightless species are the result of “*conversion* rather than *concentration*; that is, they have

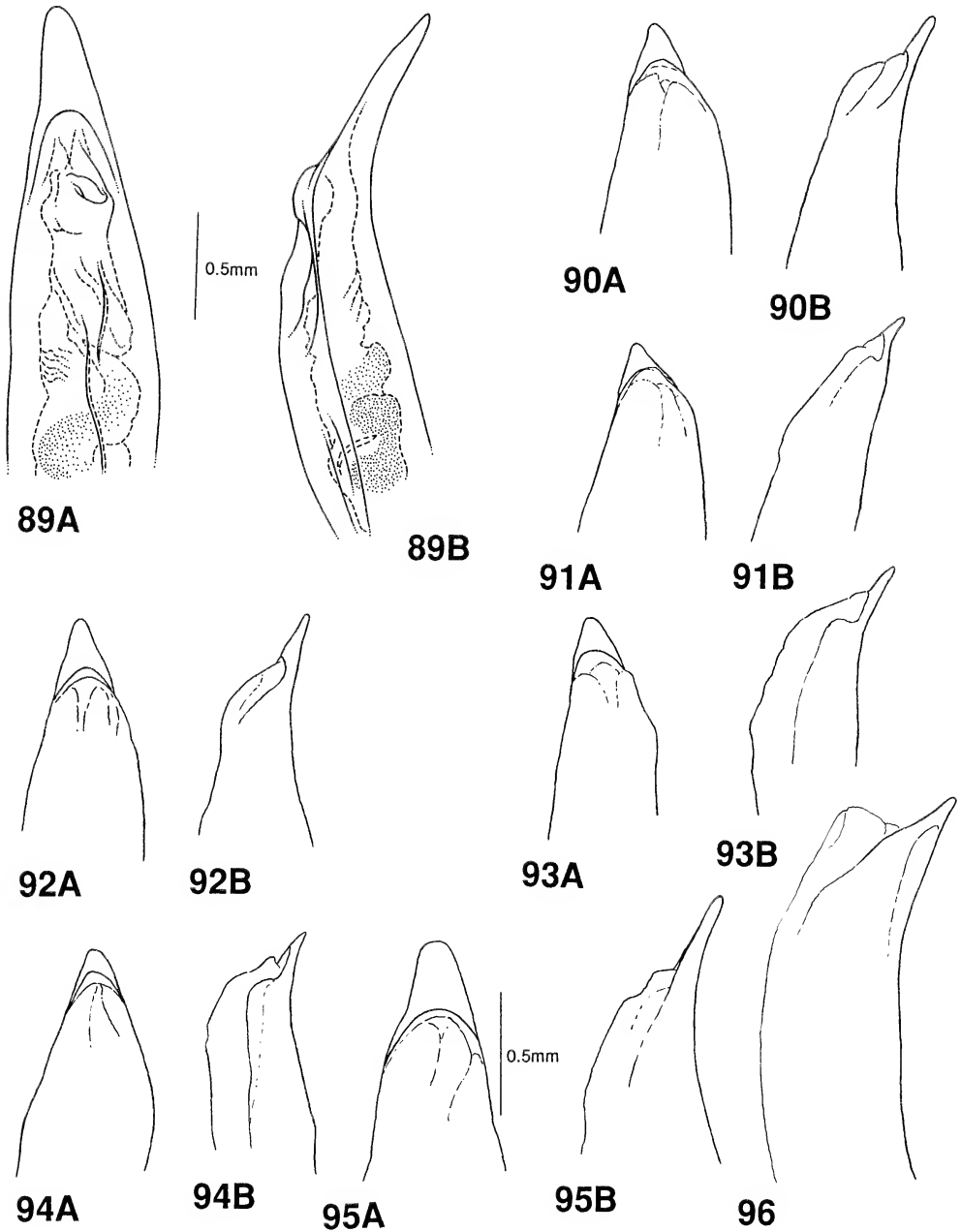


Fig. 89–96.—Line drawings of male genitalia of the *O. fulgens* species group. Fig. 89–95, median lobe, apical portion: A, B, dorsal and left lateral aspects, respectively, of: 89, *O. scintillans*, n. sp.; 90, *O. fulgens* Dejean (Orizaba, Veracruz, Mex.); 91, same (Landa de Matamoros, Queretaro, Mex.); 92, same (Tepic, Nayarit, Mex.); 93, *O. tricolor* Dejean (Jalapa, Veracruz, Mex.); 94, same (Juchaten-go, Oaxaca, Mex.); 95, *O. hoepfneri* Dejean. Fig. 96, median lobe, apical portion, left lateral aspect, of *O. sallei* Chaudoir.

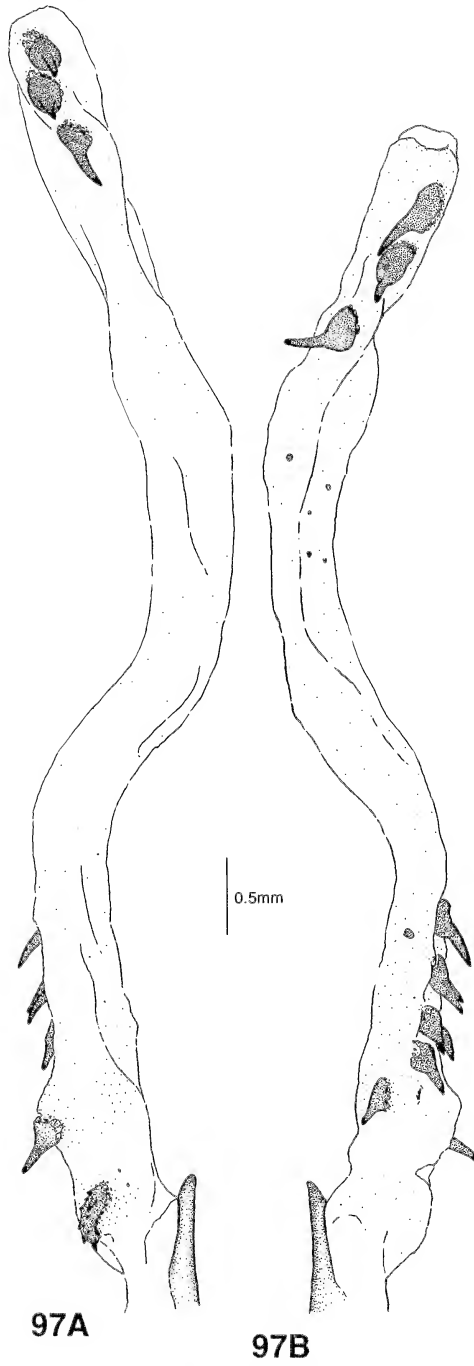


Fig. 97.—Male genitalia (median lobe, apical portion, with internal sac everted) of *Onypterygia fulgens* Dejean: A, left lateral aspect; B, right lateral aspect.

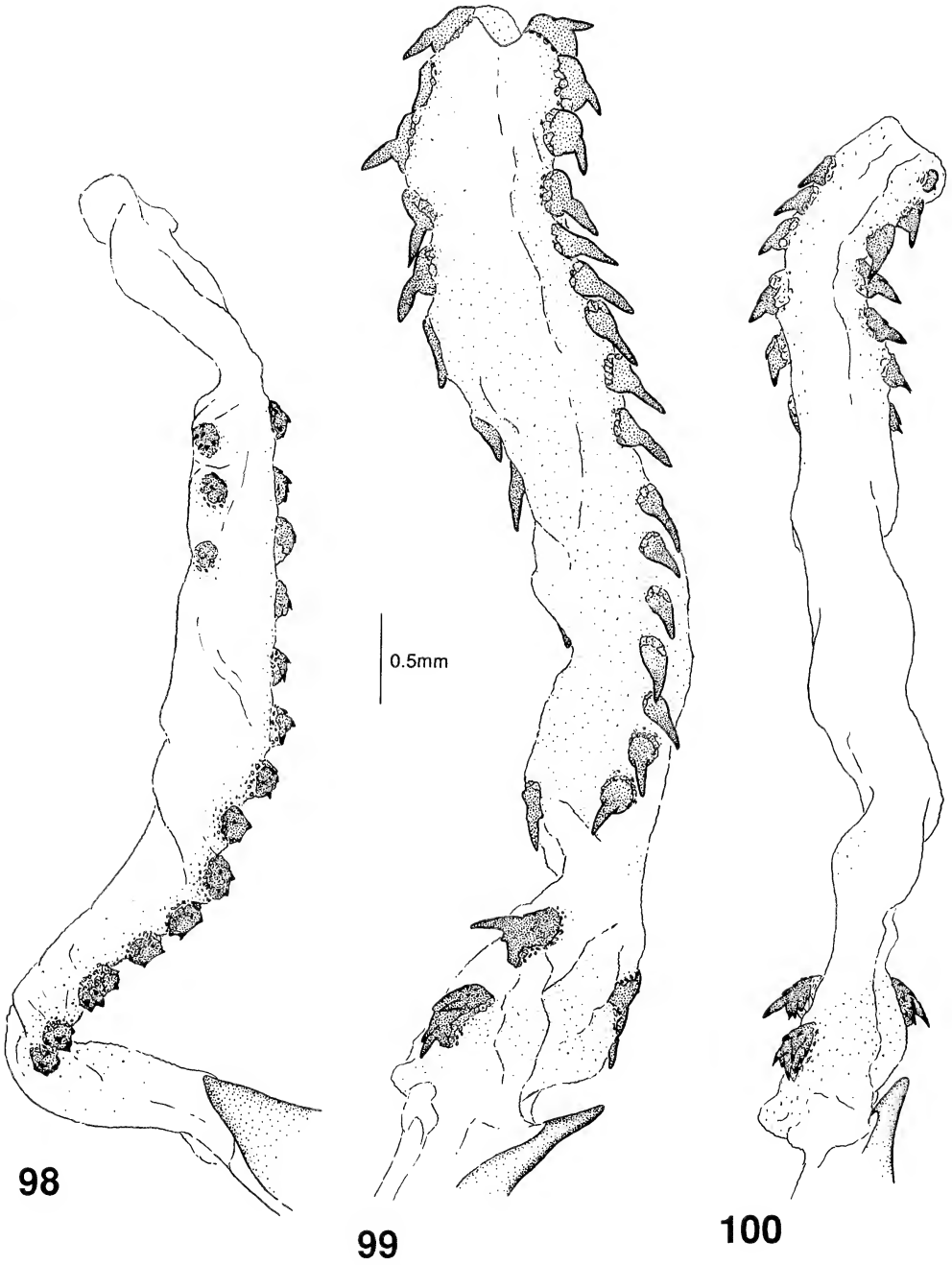


Fig. 98–100.—Line drawings of male genitalia (median lobe, apical portion, left lateral aspect, with internal sac everted) of species of the *O. fulgens* species group: 98, *O. tricolor* Dejean; 99, *O. hoepfneri* Dejean; 100, *O. sallei* Chaudoir.

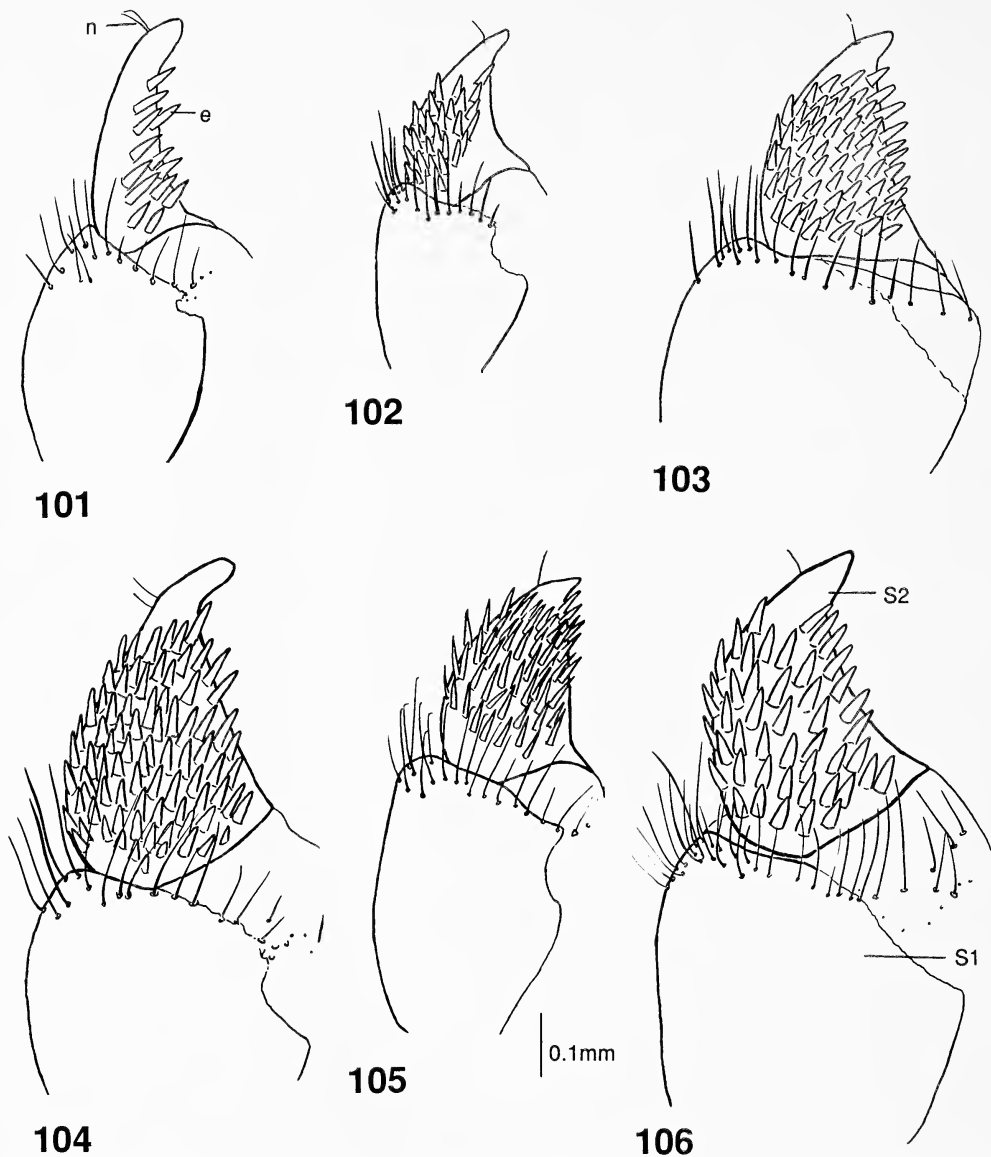


Fig. 101–106.—Line drawings of ovipositor sclerites (left stylomeres 1 and 2, left lateral aspect) of species of the *O. fulgens* species group: 101, *O. iris* Chaudoir; 102, *O. kathleenae*, n. sp.; 103, *O. polytrete*, n. sp.; 104, *O. fulgens* Dejean; 105, *O. tricolor* Dejean; 106, *O. hoepfneri* Dejean. Legend: e—ensiform seta; n—nematiform seta; S1, S2—stylomeres 1 and 2, respectively.

been produced by atrophy processes that have occurred locally [i.e., within lineages] and not by accumulation of stocks with reduced wings from other regions” (Darlington, 1971:170; see also his more general treatment of wing loss [Darlington, 1943]). However, evolution of flightlessness by wing reduction occurred independently in each lineage because macroptery in the *aeneipennis* species group (*O. pallidipes*) implies a macropterous group ancestor, whereas the bra-

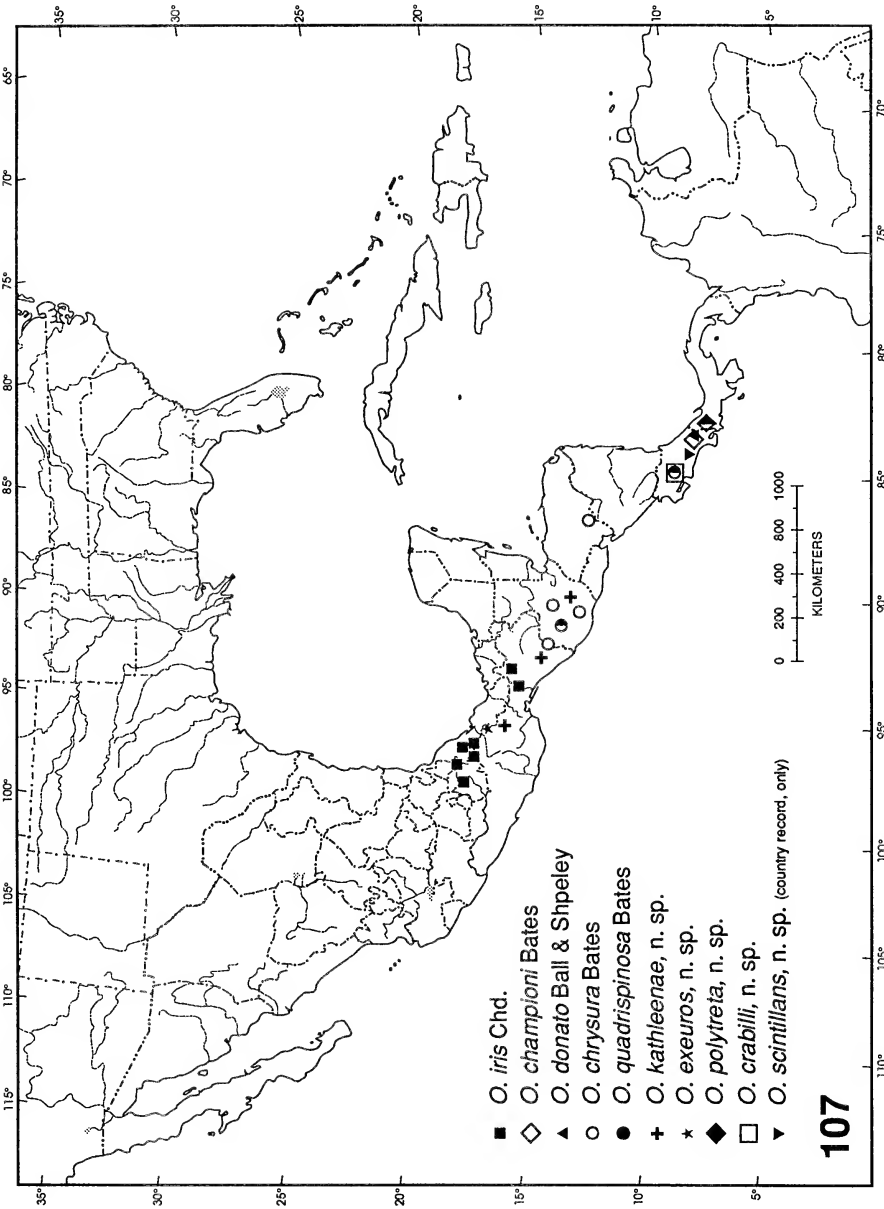


Fig. 107.—Map of southern North America, Middle, and northern South America, showing positions of collecting records for species of the *O. fulgens* species group, except *O. fulgens* Dejean, *O. tricolor* Dejean, *O. hoepfneri* Dejean, and *O. saltei* Chaudoir.

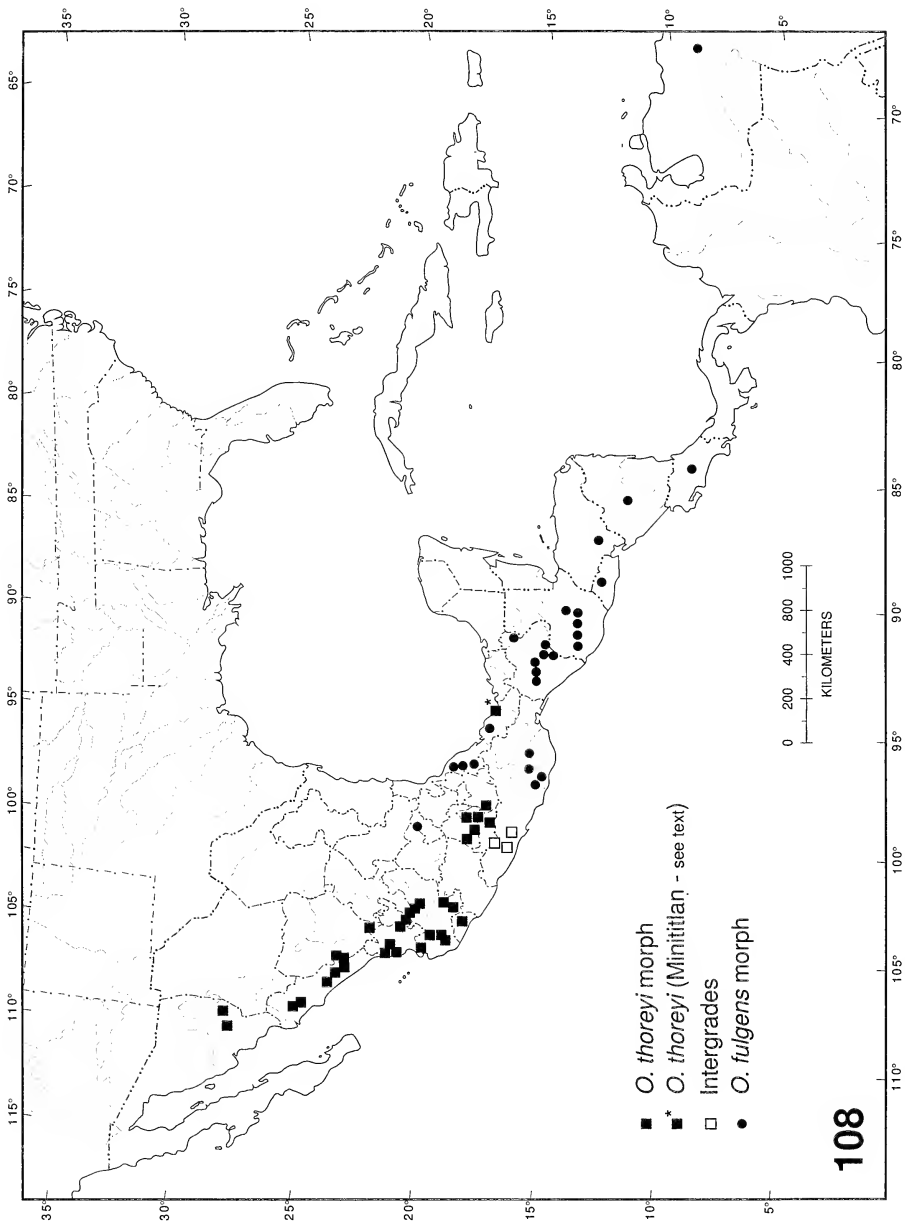


Fig. 108.—Map of southern North America, Middle, and northern South America, showing positions of collecting records for the geographical forms of *O. fulgens* Dejean; Venezuelan record excluded.

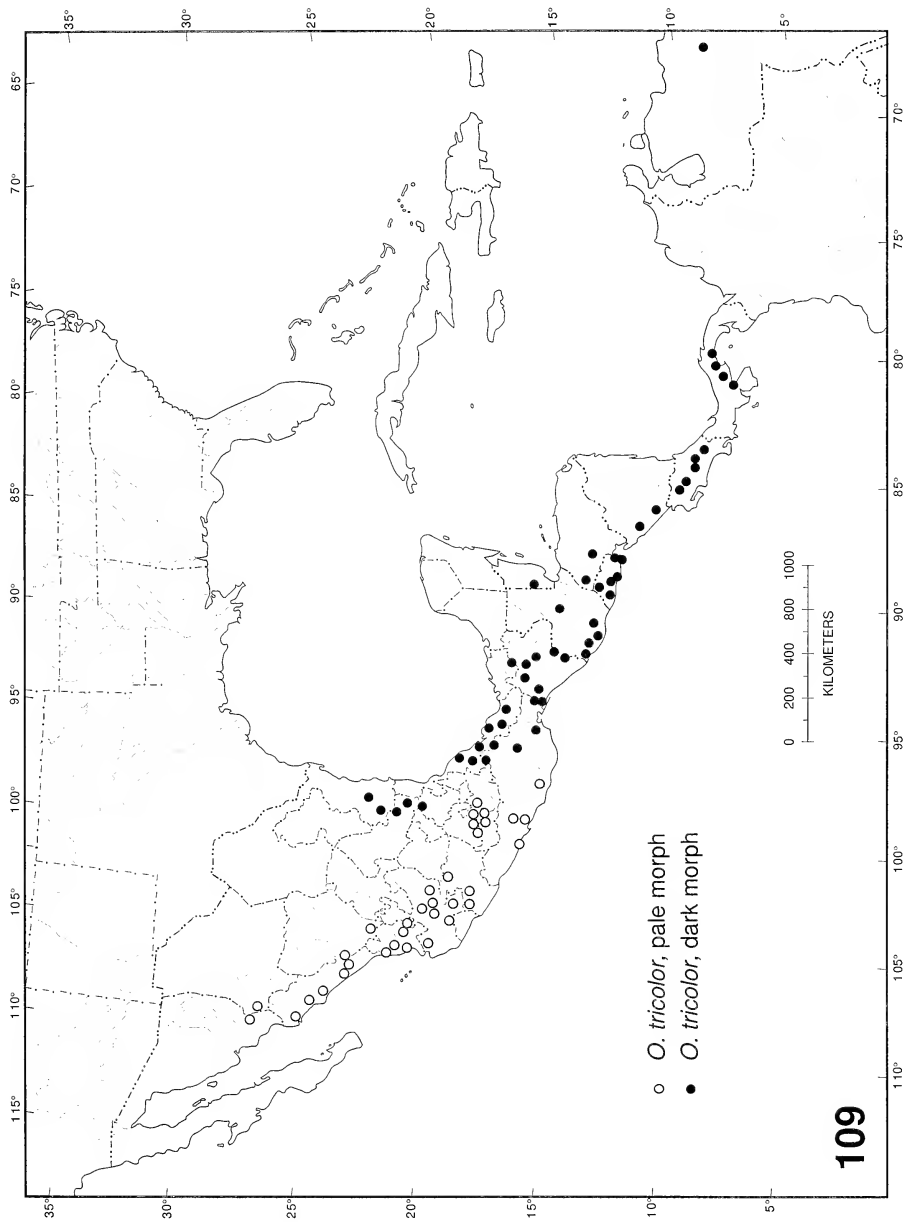


Fig. 109.—Map of southern North America, Middle, and northern South America, showing positions of collecting records for the geographical forms of *O. tricolor* Dejean; Venezuelan record excluded.

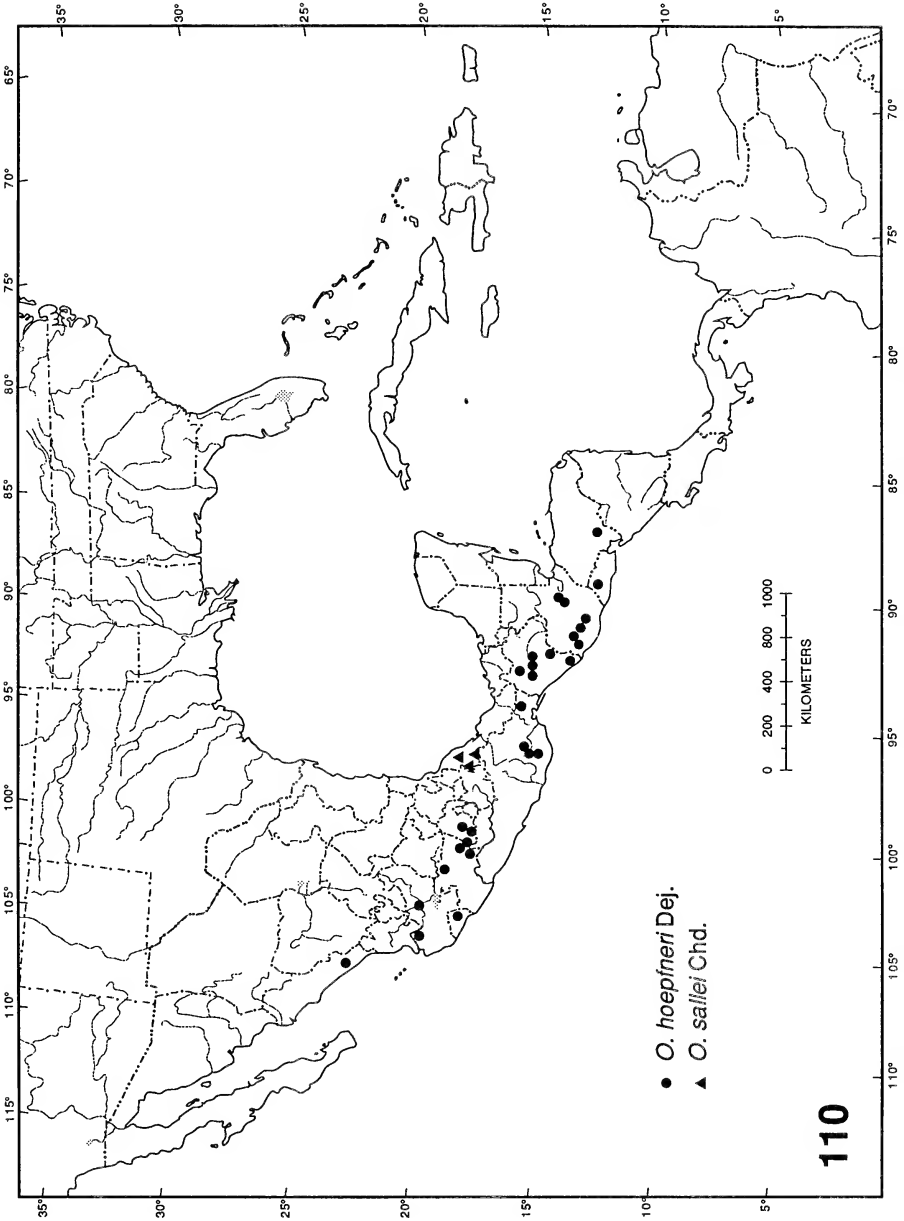


Fig. 110.—Map of southern North America, Middle, and northern South America, showing positions of collecting records for *O. hoepfneri* Dejean and *O. sallei* Chaudoir.

Table 4.—Altitudinal ranges (m above sea level), based on collecting records, of the species of *Onypterygia* Dejean.

Species	Altitudinal range	Flight wing development ¹
<i>amecameca</i>	2400	—
<i>atoyac</i>	2300	—
<i>rubida</i>	2100–2600	+, —
<i>pacifica</i>	2000–2150	—
<i>stenapteryx</i>	1700–2200	—
<i>shpeleyi</i>	1700	—
<i>wappesi</i>	1700	—
<i>cupricauda</i>	1600–1800	+, —
<i>donato</i>	1500	—
<i>polytreta</i>	1500	+
<i>pallidipes</i>	1400–2100	+
<i>crabilli</i>	1400–1550	+
<i>chrysura</i>	1400	+
<i>pseudangustata</i>	1350–2000	+
<i>longispinis</i>	1300–1900	+
<i>aeneipennis</i>	1300–1400	—
<i>championi</i>	1300	+
<i>batesi</i>	1150–2200	+, —
<i>angustata</i>	1000–2300	+
<i>hoepfneri</i>	1000–2100	+
<i>quadrispinosa</i>	1000–1500	+
<i>kathleenae</i>	900–1900	+
<i>sallei</i>	900–1500	+
<i>pusilla</i>	850–1400	+
<i>iris</i>	800–1650	+
<i>famini</i>	700–2300	+
<i>rawlini</i>	700–1550	+
<i>perissostigma</i>	600	+
<i>striblingi</i>	600	+
<i>exeuros</i>	600	+
<i>fulgens</i>	0–2500	+
<i>tricolor</i>	0–2300	+
<i>cyanea</i>	0–2200	+
<i>scintillans</i>	?	+

¹ — = Brachypterous, wings not functional as flight organs. + = Macropterous, wings functional as flight organs.

chypterous condition of all species of the *wappesi* species group indicates an immediate ancestor that was brachypterous.

We postulate further that the *wappesi* and *aeneipennis* species groups are among the more basal (i.e., closer to ancestral *Onypterygia*) and that their present confinement to higher altitude is consistent with taxon cycle (Wilson, 1961) or taxon pulse (Erwin, 1979, 1985) theory, which predicts the restriction of ranges, and ecological amplitudes of the more ancestral taxa of lineages. In contrast, the more derived (postulated to be later-evolving) lineages of *Onypterygia* exhibit more extensive altitudinal ranges (Table 4). The species of some species pairs of adelphotaxa differ from one another in altitudinal distribution (cf. especially *O. shpeleyi*–*pacifica*, *O. pallidipes*–*rubida*, *O. rawlini*–*pusilla*, and *O. kathleenae*–*exeuros*), suggesting range reduction and subsequent specialization of vicars of wider-ranging ancestral stocks.

Habitat

Forest-associated, the ecological range of the species of *Onypterygia* extends from dry, lowland tropical forest (“Bosque Tropical Subcaducifolio,” “Bosque

Tropical Caducifolio,” and “Bosque Espinoso” [Rzedowski, 1978]) to higher-altitude moist to wet tropical montane forest (“Selva Alta o mediana subperennifolia” [Sarukhan, 1968]) to cloud, oak–pine, and pine–fir forests (“Bosque de coníferas y de *Quercus*” and “Bosque Mesófilo de Montana” [Rzedowski, 1978]). Most species live in trees or low bushes and vines in montane tropical, to oak–pine forests. Evidently, the higher altitude cold fir forests have been invaded only marginally. The ecological range of two species, *O. fulgens* and *O. tricolor*, extends from tropical deciduous to at least oak–pine forests. *Onypterygia cyanea*, of the *O. famini* species group, tends to occupy and may be restricted to relatively dry forests, at lower altitudes.

Extensive range overlap is common, especially among species not very closely related. For example, during a short trip to the mountains of Guatemala, during the period May 19–June 13, 1991, six species of *Onypterygia* that represented four species groups were encountered. Eleven localities were sampled, some only at night, some during daylight.

Of these species, *O. pusilla* was represented by a single specimen, *O. tricolor* by three specimens at one locality, and *O. famini* by six specimens taken at UV light, at one locality. Three species, *O. angustata*, *O. longispinis*, and *O. fulgens*, were encountered more commonly.

Range overlap was extensive in the montane tropical and oak–pine forests. In the higher altitude, colder, oak–pine forests in the vicinity of Guatemala City, only *O. angustata* was found. Conversely, this species seemed relatively scarce at altitudes less than 1650 m, whereas another member of the *angustata* species group, *O. longispinis*, was encountered frequently at the lower altitude.

Had we collected in these localities at other times in the year, or under other climatic conditions, the results might have been different, in that the less frequently collected species may have been more common. Regardless, the relative scarcity of three of the species may be evidence of ecological differentiation within *Onypterygia*, just as the somewhat different distribution of *O. angustata* and *O. longispinis* is suggestive of ecological differentiation within one species group. Similarly, although the ranges of *O. fulgens* and *O. tricolor* overlap extensively throughout Middle America, during our time in Guatemala the former was relatively abundant and the latter very scarce.

The three common species were encountered both by night (principally at UV light) and by day. Occurrence at light suggests night flight, and thus nocturnal activity. The beetles were not seen running or flying during the day (they were taken principally by beating vegetation [green leaves] and by removing epiphytes and various types of debris associated with living trees), and may not have been active then.

Conclusions

The limited ecological data available, especially altitudinal range, show some differences among evolutionarily significant groups of taxa (for example, at the level of species group and species pairs of adelphotaxa). We take this as evidence for ecological differentiation in the course of development of the extant assemblage of species of *Onypterygia*.

Evolutionary Considerations

Structural Features

Based on the notion of a generalized member of the subtribe Platynina, to which *Onypterygia* belongs, we postulate some trends in structural features. Setae have

been lost from the pronotum and elytral disc, and have been gained, principally on abdominal sternum VII. The elytra have been modified through development of apical and sutural spination, development (and probably subsequent reduction) of a posterolateral callus, development of large pits in the discal surfaces, and foveate umbilical and discal setigerous punctures, and reduction of interneurs. Hind wings have been reduced (with consequent loss of ability to fly), and as well, the metathorax has been reduced. Tarsomeres have been modified, principally tarsomere 4, by lengthening of the outer apical lobe.

The male genitalia exhibit striking modifications, principally in size of internal sac and in its armature. Two types of armature have developed (spinose setae and setose spines), and show trends both to increased complication and loss.

Female ovipositors have been modified also, principally in form (from falcate to lobate) and in setation of stylomere 2 (from few to numerous ensiform setae, on the lateral surfaces). The reproductive tract itself evidently was modified, with potential lengthening of the bursa copulatrix, in correlation with lengthening of the male internal sac. Body colors exhibit substantial variation, by individual part and by total pattern of each species. However one interprets evolution of color, substantial homoplasy will have to be postulated.

Tarsal claws exhibit two conditions: pectinations more, or less, numerous. The latter condition characterizes one species only, *O. perissostigma*, which is enigmatic in a number of other features, too. The lower number of pectinations could represent reduction and be thereby apotypic, or could represent the original condition for *Onypterygia*, and thus be plesiotypic. We decline to make further comment now.

Structural Features and the Species Groups

The species groups are designated, rather arbitrarily, as basal or derived. More basal are the *famini*, *wappesi*, *aeneipennis*, and *pusilla* groups. The more derivative are the *angustata* and *fulgens* groups, with the most markedly derived features in the latter group. The *perissostigma* group occupies an intermediate position, although we regard it as basically primitive.

Geographical History

Introduction.—The known geographical ranges of the species of *Onypterygia* are basic empirical components of this analysis (Fig. 27, 33, 46, 52, 62, and 107–110). Also, a general theory of evolution of distribution patterns of Neotropical taxa is used that has been developed during the past half century by biogeographers and geologists; see, in particular, Whitehead (1976), Schreiber (1978), Erwin (1979), Noonan (1979, 1988), Savage (1982), and Halffter (1987). For zoogeographical analyses of taxa of Carabidae with ranges comparable to those of *Onypterygia*, see references in Noonan (1985) and Liebherr (1991a, 1991b, 1994).

Distribution Patterns.—At the generic level, the distribution pattern of *Onypterygia* is designated here as “the Meso-American Montane Pattern” of Halffter (1987:107). This is an assumption, based on the general similarity of the distribution pattern to that of the *Platynus degallieri* group (Liebherr, 1994:843). The adelphotaxon of *Onypterygia* may have been South American or Middle American in origin. As a member of the Meso-American Montane assemblage, the time of origin of *Onypterygia* is postulated reasonably as Oligocene–Miocene (Liebherr, 1992:108), or between, say, 20 and 30 million years before present.

The distribution pattern of *Onypterygia* is presented in terms of species diver-

Table 5.—*Number of species of Onypterygia Dejean, by 5°-intervals of latitude.*

Latitude	Number of species
25–30	3
20–25	6
15–20	24
10–15	14
5–10	9

sity and postulated interspecific relationships. A general synthesis is based on correlating the chorological patterns and the relationship of some of the species.

Latitudinally species number (Table 5) is minimal toward the north, with the ranges of only three species extending north of the Tropic of Cancer; the northernmost record for *O. hoepfneri* is either just slightly north of or slightly south of that line; being marginal, it was excluded from the group of species whose ranges extend farther north. Numbers are maximal in central Mexico and decrease into lower Central America. Only two species, *O. fulgens* and *O. tricolor*, are known to enter South America, and their ranges do not extend as far south as the Amazon Basin.

The ranges of about two-thirds of the species are confined to a single 5°-unit (Table 6), with a marked decrease in numbers to a single species that ranges through all five units. The longitudinal component of the distribution pattern is shown by numbers of species with ranges confined to either the Pacific Versant (16 species) or the Atlantic Versant (seven species). In summary, the distribution of *Onypterygia* is principally tropical and almost exclusively Middle American. Most species have restricted ranges, and species are more numerous on the Pacific than on the Atlantic Versant.

In his study of cladistic-biogeographic patterns of distribution of montane Middle American Carabidae, Liebherr (1994) recognized a series of “areas of endemism,” based in part on geological considerations. With modifications and refinements indicated below (Table 7), these areas (Fig. 111) are used here to describe distribution patterns of the species of *Onypterygia*. The term “endemism” is replaced here with *precinctin*, a noun derived from the adjective *precinctive* (Frank and McCoy, 1990, 1995; see also Shpeley and Ball, 1994:18).

Liebherr (1994:847, fig. 4) recognized five northern areas. In the absence of northern *precinctive* taxa of *Onypterygia*, four of these areas are combined as the Sierra Madre Occidental. The Sierra Madre Oriental is distinguished because of its different composition of *Onypterygia* species. Liebherr’s “Sierra Transvolcanica” is divided into two parts. Similarly, the “Sierra Madre del Sur” system is divided into three areas, although the collective term is used as necessary, or convenient.

Table 6.—*Number of species of Onypterygia Dejean by number of 5°-intervals of latitude occupied.*

Number of units occupied	Number of species
One	22
Two	6
Three	3
Four	2
Five	1

Table 7.—*Areas of precinction (= endemism) inhabited by the species of Onypterygia Dejean.*

Liebherr (1994) system	Present system
Arizona Mountains	
Sonoran Desert	
Sierra Madre Occidental	Sierra Madre Occidental
Sierra Madre Occidental (S)	Sierra Madre Oriental
Sierra Madre Oriental	Sierra Transvolcanica East
	Sierra Transvolcanica West
Sierra Transvolcanica	Sierra Madre de Oaxaca
Sierra Madre del Sur	Sierra de Atoyac
	Sierra de Miahuatlan
Chiapan–Guatemalan Highlands	Chiapan–Guatemalan Highlands
Talamancan Cordillera	Talamancan Cordillera

Based on Binford (1989:352, fig. 31), the Sierra Madre de Oaxaca includes the Sierra de Juárez, the Sierra Aloapaneca, and the Sierra de Zempoaltepec; and “Sierra de Atoyac” is used for that part of the Sierra Madre del Sur located in the state of Guerrero. For convenience, the term “Sierra de Miahuatlán” is used to include that range as well as the Sierra Yucuyácu and the Sierra de Cuatro Venados, all three ranges being in the Pacific drainage systems of Oaxaca, in contrast to the Atlantic drainage system, in which the Sierra Madre de Oaxaca is located. These modifications are based on the restricted known ranges of many of the species of *Onypterygia*. The “Chiapan–Guatemalan Highlands” and “Talamancan Cordillera” are accepted as delimited by Liebherr.

Group occupancy ranges from one (*perissostigma* species group—Sierra de Juárez, in the Sierra Madre de Oaxaca) to all nine areas of precinction, with most groups occupying at least six areas (Table 8). The *fulgens* group has representative taxa in all areas. Most areas of precinction have from four to six of the seven species groups of *Onypterygia*. The Sierra Madre de Oaxaca and the Sierra Transvolcanica West have the most species groups, while the Sierra Madre Occidental and Talamancan Cordillera have the least.

The species of the more basal lineages (Subtotal A) are concentrated in the Sierra Transvolcanica West and Sierra de Atoyac, whereas the species of the more derived lineages (Subtotal B) are more numerous in the Chiapan–Guatemalan Highlands and Talamancan Cordillera (Tables 9–11). The northern areas (Sierra Madre Occidental, Sierra Madre Oriental) are without precinctive species. The Talamancan Cordillera has the largest number (five), followed by the Sierra Transvolcanica West and the Sierra Madre de Oaxaca, with four each. Generalizing the pattern by combining with themselves the parts of the Sierra Transvolcanica and the Sierra Madre del Sur, the pattern of precinction from northern Mexico to Panama is: 0–6–9–1–5. This illustrates the numerical preponderance of the Sierra Madre del Sur (with nine precinctive species), followed by that of the Sierra Transvolcanica (six precinctives). Most species (22) are known from (and possibly confined to) single areas of precinction (Table 12). Only two species are known from all areas. Eleven species are represented in two to seven areas of precinction.

Lowlands separate the adjacent areas of precinction from one another. These are regarded as topographical barriers that restrict the movements of taxa occupying the areas of precinction (Fig. 111). The Isthmus of Tehuantepec, for purposes of analysis, is treated as two barriers, one for the Pacific Versant and one

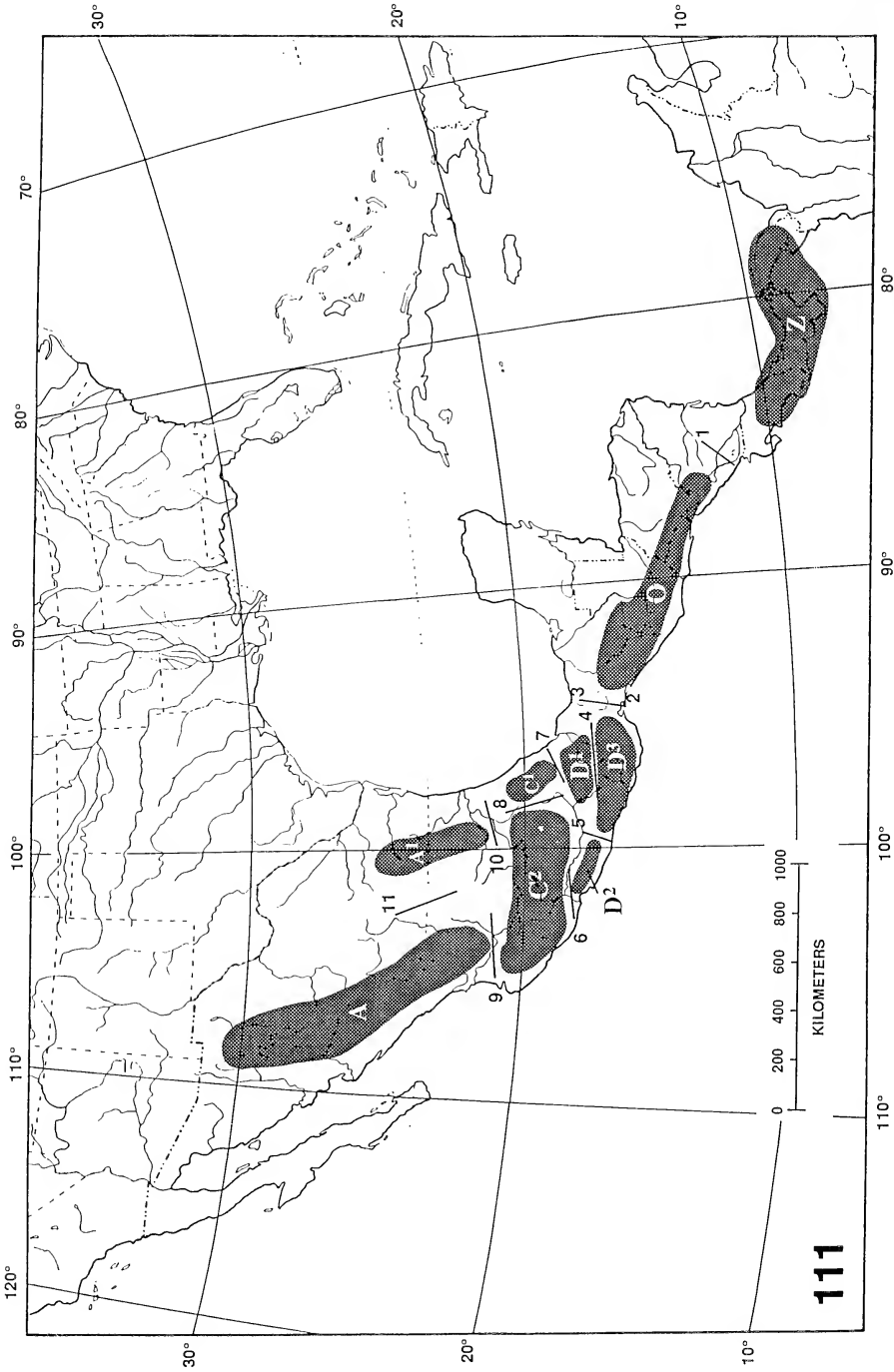


Fig. 111.—Map of southern North America, Middle, and northern South America, showing positions of Middle American areas of precinction modified from Liebherr (1994), and the postulated topographical barriers (represented by numbered lines) between adjacent areas. See text for further details. Legend: A, Sierra Madre Occidental; A', Sierra Madre Oriental; C¹, Sierra Transvolcanica East; C², Sierra Transvolcanica West; D¹, Sierra Madre de Oaxaca; D², Sierra de Atoyac; D³, Chiapan-Guatemalan Highlands; O, Chiapan-Guatemalan Highlands; Z, Talamancan Cordillera.

Table 8.—Distribution of the species groups of *Onypterygia* Dejean in relation to areas of precinction.

Areas of precinction	Species group ¹							Total number groups/area
	<i>per</i>	<i>wap</i>	<i>aen</i>	<i>fam</i>	<i>pus</i>	<i>ang</i>	<i>ful</i>	
Sierra Madre Occidental				X			X	2
Sierra Madre Oriental			X	X	X	X	X	5
Sierra Transvolcanica East			X	X	X	X	X	5
Sierra Transvolcanica West		X	X	X	X	X	X	6
Sierra Madre de Oaxaca	X		X	X	X	X	X	6
Sierra de Atoyac		X	X	X	X		X	5
Sierra de Miahuatlan		X	X	X	X	X	X	6
Chiapan–Guatemalan Highlands				X	X	X	X	4
Talamancan Cordillera						X	X	2
Total areas occupied/group	1	3	6	8	7	7	9	

¹ Abbreviations of names of species groups: *aen*, *aeneipennis*; *ang*, *angustata*; *fam*, *famini*; *ful*, *fulgens*; *per*, *perissostigma*; *pus*, *pusilla*; and *wap*, *wappesi*.

for the Gulf Versant. Twelve species have crossed one or more of these barriers, probably in Recent time (Table 13).

No species have crossed the Mexican Plateau north of the Sierra Transvolcanica (Barrier No. 11), and relatively few species have crossed the Nicaraguan Depression (Barrier No. 1), supporting Halffter's (1987:107) assessment (Table 13). In contrast, Barrier No. 10 (the lowlands and low mountains between the Sierra Madre Oriental area of precinction and the Sierra Transvolcanica East) has been crossed by most of the extant species of *Onypterygia* in the region.

The Isthmus of Tehuantepec (Barrier 2–3) has been crossed relatively frequently, as one might expect from Halffter's (1987:108) estimate of the strength of this barrier for tropical-adapted species. In the past, the situation might have been quite different, with so much of the evolution of the *fulgens* species group having occurred to the southeast of this barrier.

Although the species *O. fulgens* and *O. tricolor* are both widespread, their geographical differentiation (Fig. 108, 109) may be viewed as evidence that their extensive ranges developed in pre-Recent (probably Pleistocene) time, and were separated into northwestern and southeastern vicariads leading to infraspecific differentiation. Because of the extensive ranges of these two species, the putative refugia of the infraspecific morphs cannot be estimated.

Evolutionary Correlations.—These correlations are sought for both species groups and species. The more derived, or younger groups are the more widespread (Table 8), just as many of the more structurally derived species are the most widespread (Table 10). The older species groups are concentrated in the Sierra Transvolcanica and the Sierra Madre del Sur, whereas the more recent groups are best represented in the more southern precinctive centers.

Seven pairs of species-level adelphotaxa exhibit allopatric patterns (Table 14). One pair (*pallidipes*–*rubida*) has differentiated within a single area of precinction (Sierra Transvolcanica West). For the remaining six pairs, one can infer differentiation between areas of precinction, or if within, then between different parts of that area: *championi*–*donato* and *polytreta*–*crabilli*, different parts of the Talamancan Cordillera; *shpeleyi*–*pacifica*, Sierra de Atoyac and Sierra de Miahuatlán; *hoepfneri*–*sallei*, Sierra Transvolcanica East and West; and *pseudangustata*–*striblingi*, Sierra Transvolcanica East and Sierra Madre de Oaxaca. Differentiation of the species pair *pusilla*–*rawlinsi* may have occurred within the Sierra Transvol-

Table 9.—*Distribution of the species of the perissostigma, wappesi, aeneipennis, famini, and pusilla species groups of Onypterygia Dejean, in relation to areas of preinction.*

Areas of preinction	Species ¹															Subtotal A species/area	
	per	wap	ame	ato	shp	pac	bat	aen	cup	ste	pal	rub	fam	cya	raw		pus
Sierra Madre Occidental														X			1
Sierra Madre Oriental							X						X			X	3
Sierra Transvolcanica East							X						X			X	3
Sierra Transvolcanica West			X				X			X	X	X	X	X	X		9
Sierra Madre de Oaxaca	X						X						X	X		X	4
Sierra de Atoyac		X		X	X				X				X			X	7
Sierra de Miahuatlan						X		X					X			X	4
Chiapan-Guatemalan Highlands													X			X	2
Talamancan Cordillera																	
Subtotal A																	
Number of areas occupied/species	1	1	1	1	1	1	4	1	1	1	1	1	7	3	1	7	

¹ Abbreviations of specific epithets: *aen*, *aeneipennis*; *ame*, *amecameca*; *ato*, *atoyac*; *bat*, *batesi*; *cup*, *cupricauda*; *cya*, *cyanea*; *fam*, *famini*; *pac*, *pacific*; *pal*, *pallidipes*; *per*, *perissostigma*; *pus*, *pusilla*; *raw*, *rawlini*; *rub*, *rubida*; *shp*, *shpeleyi*; *ste*, *stenapteryx*; and *wap*, *wappesi*.

Table 10.—*Distribution of the species of the angustata and fulgens species groups of Onypterygia Dejean, in relation to areas of precinction.*

Areas of precipitation	Species ¹																		Subtotal B species/area
	lon	ang	pse	str	iri	cha	don	chr	kat	exe	pol	cra	qua	sci	ful	tri	hoe	sal	
Sierra Madre Occidental															X	X	X		3
Sierra Madre Oriental		X													X	X			3
Sierra Transvolcanica East		X	X		X										X	X		X	6
Sierra Transvolcanica West		X													X	X	X		4
Sierra Madre de Oaxaca				X					X	X					X	X	X		6
Sierra de Atoyac															X	X	X		3
Sierra de Miahuatlan		X						X	X						X	X	X		4
Chiapan-Guatemalan Highlands	X	X			X								X		X	X	X		9
Talamancan Cordillera		X				X	X	X		X	X	X	X	X	X	X			10
Subtotal B																			
Number of areas occupied/species	1	6	1	1	2	1	1	2	2	1	1	1	2	1	9	9	6	1	

¹ Abbreviations of specific epithets: *ang*, *angustata*; *cha*, *championi*; *chr*, *chrysura*; *cra*, *crabilli*; *don*, *donato*; *exe*, *exeuro*; *ful*, *fulgens*; *hoe*, *hoepfneri*; *iri*, *iris*; *lon*, *longispinis*; *kat*, *kathleenae*; *pse*, *pseudangustata*; *pol*, *polyreta*; *qua*, *quadriscopiosa*; *sal*, *sallei*; *sci*, *scintillans*; *str*, *striblingi*; and *tri*, *tricolor*.

Table 11.—Total number of species of *Onypterygia* per area of precinction. Data derived from tables 9 and 10.

Areas of precinction	Number of species		A + B
	Subtotal A	Subtotal B	
Sierra Madre Occidental	1	3	4
Sierra Madre Oriental	3	3	6
Sierra Transvolcanica East	3	6	9
Sierra Transvolcanica West	9	4	13
Sierra Madre de Oaxaca	4	6	10
Sierra de Atoyac	7	3	10
Sierra de Miahuatlan	4	4	8
Chiapan-Guatemalan Highlands	2	9	11
Talamancan Cordillera	0	10	10

canica West, where both species are represented, or between the latter and one of the other areas in which *O. pusilla* is represented, but not *O. rawlinsi*.

One species pair (*famini-cyanea*) exhibits a parapatric distribution pattern, with the ranges of both species in contact or nearly so, in the Sierra Madre de Oaxaca and Sierra Transvolcanica West. However, *O. cyanea* occupies drier areas than those occupied by *O. famini*. Also, the range overlap is not total, each species occupying different areas in the northern parts of their respective ranges.

Three species pairs are at least partly sympatric, with overlapping ranges in the Sierra Madre de Oaxaca (*kathleenae-exeueros*), or the Talamancan Cordillera (*championi-donato*, *quadriscopiosa-scitillans*).

One set of six species (the *aeneipennis* species group) involves principally allopatric and parapatric affinities, with partial sympatry among the older members; and one set of four species (*longispinis-angustata-pseudangustata* + *striblingi*) involves principally allopatry, with partial sympatry exhibited by the two older species. In only one species group (*fulgens*) is sympatry extensive.

In summary, allopatry, parapatry, or partial sympatry are the dominant types of distribution patterns among the more closely related species of *Onypterygia*. Among the more distantly related (i.e., those that are less similar to one another in structural features) species and species groups, more or less extensive sympatry is the rule.

Area Affinities.—In general, the distribution patterns of the moderately wide-spread species and older (more basal) species groups (Table 9) indicate a close

Table 12.—Number of species of *Onypterygia* Dejean in relation to number of areas of precinction occupied. Data derived from tables 9 and 10.

Number of areas of precinction occupied	Number of species
One	22
Two	4
Three	1
Four	1
Five	0
Six	2
Seven	2
Eight	0
Nine	2

Table 13.—Distribution of wider-ranging species of *Onypterygia* Dejean, in relation to crossed topographical barriers between adjacent areas of precinction. The number of barriers crossed is expressed as a percentage of the total number of species (less those known from a single locality, only) that occur on each side of the barrier in adjacent areas of precinction. Each percentage is accepted as representing roughly the relative strength of the barrier in question.

Species	Barrier number ¹											Total number of barriers crossed
	11	9	1	8	6	4	3	5	7	2	10	
<i>chrysura</i>			X									1
<i>quadrispinosa</i>			X									1
<i>iris</i>									X	X		2
<i>kathleenae</i>							X				X	2
<i>batesi</i>		X			X				X			2
<i>cyanea</i>			X	X		X		X		X		2
<i>angustata</i>		X			X	X	X	X		X		5
<i>hoepfneri</i>				X	X	X	X	X	X	X	X	6
<i>famini</i>				X	X	X	X	X	X	X	X	7
<i>pusilla</i>		X	X	X	X	X	X	X	X	X	X	8
<i>fulgens</i>		X	X	X	X	X	X	X	X	X	X	10
<i>tricolor</i>		X	X	X	X	X	X	X	X	X	X	10
Total number of species crossing	0	4	5	5	6	6	6	5	6	8	5	
Total species available ²	6	9	11	10	12	11	11	9	11	13	7	
% total available species crossing barrier	0	44	45	50	50	54	54	56	54	61	71	

¹ For positions of barriers, see Fig. 111.
² Total number of species adjacent to barrier.

Table 14.—Species-level adelphotaxa of Onypterygia Dejean and their chorological affinities.

Figure number	Species pairs	Geographic association		Putative barriers or areas of contact
		Parapatric	Allopatric	
33	<i>shpelevyi-pacifica</i>		X	between D ² and D ³ (barrier number 5)
27	<i>famini-cyanea</i>	X		between C ¹ and C ² (barrier number 8) within D ³
110	<i>hoepfneri-sallei</i>		X	between C ¹ and C ² (barrier number 8)
62	<i>pseudangustata-striblingi</i>		X	between C ¹ and D ¹ (barrier number 7)
52	<i>rawlini-pusilla</i>		X	within C ²
46	<i>pallidipes-rubida</i>		X	within C ²
107	<i>kathleenae-exeuos</i>	X		within D ¹
107	<i>quadrispinosa-scinillans</i>	X		within Z
107	<i>championi-donato</i>		X	within Z (secondary overlap)
107	<i>polytreta-crabilli</i>		X	within Z

affinity between the adjacent Sierra Transvolcanica and Sierra Madre del Sur. Similarly, the distribution patterns of pairs of adelphotaxa (Table 14) indicate a marked affinity between the Chiapan–Guatemalan Highlands and the Talamancan Cordillera. The *famini* and *pusilla* species groups indicate an affinity among the Transvolcanic, Oaxacan, and Chiapan–Guatemalan areas of precinction, and places the Talamancan area in isolation. In contrast, marked affinity is exhibited between the Chiapan–Guatemalan Highlands and the Talamancan Cordillera by the concentration therein of the *fulgens* group in general, and in particular by the species-pair *quadrispinosa*–*scintillans*, and the triad *iris*–*championi* + *donato*. For the northern areas, the distribution of species groups indicates a closer affinity between the Sierra Madre Oriental area and the southern areas than between the latter and the Sierra Madre Occidental. The overall pattern is indicative of concentration of seemingly older centers of differentiation in the Sierra Transvolcanica and Sierra Madre del Sur, with a more recent center in the Talamancan Cordillera. Also indicated is continued differentiation in the older centers, leading in them to a combination of comparatively recently evolved species and older lineages.

Chorological Scenario.—The data about geographical distribution of the species of *Onypterygia* suggest cyclic vicariance (Noonan, 1988:377–378). As formulated by Ball and Nimmo (1983:344–345) this hypothesis is based on a postulated sequence of alternating periods of favorable and unfavorable climates (or other circumstances), with resident taxa being alternately widespread during favorable periods, and with restricted ranges during unfavorable periods. Restricted areas for survival during unfavorable periods are refugia; these persist, to function again and again as survival centers. During unfavorable periods, the ranges of taxa are fragmented into isolated vicarages provided by the refugia, and in isolation the resulting vicars undergo differentiation that can lead to speciation. During favorable periods, the taxa become widespread by dispersal, with consequent increase in diversity in areas of overlap of previously isolated groups. This hypothesis was used by Peck (1973:150–156, note especially fig. 216) to explain evolution of the Appalachian species of *Adelops*, and is applicable to the distribution patterns of a variety of Neotropical taxa (see, for example, Haffer, 1982:9).

Applied specifically to *Onypterygia*, mesic montane tropical forests at 1000 to 1500 m altitude are interpreted as the refugial areas for the species. The lower slopes were invaded and lowland intermontane barriers likely were crossed during especially favorable (with more rainfall?) climatic periods.

The early evolution of species groups likely was concentrated to the north of the Isthmus of Tehuantepec because the ranges of the more basal stocks are concentrated there. Possibly in late Miocene–early Pliocene time, that barrier (No. 2–3, Fig. 111) was crossed by one lineage of *Onypterygia* that spread southeastward, entering the Chiapan–Guatemalan Highland system and Talamancan Cordillera (across the Nicaraguan Depression—Barrier No. 1), and differentiating to form the *angustata* and *fulgens* species groups. That differentiation might have involved two vicariance events: one, between the Oaxaca mountains and the more southern ranges, and the second, between the Chiapan–Guatemalan Highlands and the Talamancan Cordillera. Invasion of the latter mountain system might not have taken place until Pliocene time, with formation of land connections between nuclear and lower Central America.

Continued climatic fluctuations through Late Tertiary and Quaternary time influenced the ebb and flow of the *Onypterygia* populations and their differentiation.

Under ecologically favorable conditions, species were more widespread; under unfavorable conditions, they were restricted to montane refugia, when differentiation of formerly conspecific vicars took place. The most recent events, probably, were the invasion of the western slopes of the northern Sierra Madre Occidental by species of the *famini* and *fulgens* groups, and the invasion of northern South America by at least two species of the latter group only. Preceding these invasions, both *O. fulgens* and *O. tricolor* had differentiated partially, each represented by a pair of geographically distinctive morphs.

Although range restriction alternating with expansion provides the physical basis for development of diversity overall, the system does not account for continued restriction of species to single mountain systems. Only those taxa become widespread that have the adaptations to use the favorable conditions to enter the lowlands. The species *O. fulgens* and *O. tricolor*, for example, evidently had the necessary adaptations, and became very widespread, although probably over an extended period involving more than one cycle of favorable-unfavorable conditions. This is shown by the marked intraspecific differentiation exhibited by each of them, that probably developed during an isolation phase that preceded the Holocene Epoch.

In contrast, the members of the *wappesi* and *aeneipennis* species groups probably are becoming bound to montane habitats, as shown by wing loss and seeming restriction to higher altitudes. This does not preclude intramontane differentiation within a single mountain system or massif.

CONCLUSION

Some 166 years have elapsed since *Onypterygia* was named as a genus of Carabidae by P. F. M. A. Dejean, and it is 117 years since the genus was last revised by Maximilien de Chaudoir. Henry Walter Bates, some 113 years ago, placed those species plus additional species that he discovered in the general context of the Middle American insect fauna, as he knew it. The present contribution has focused on making known the work of these illustrious predecessors, and placing it in the context of what new knowledge we have been able to acquire, thanks to the efforts of many colleagues, as well as our own explorations, in Mexico.

We have provided also the beginning of a basis in evolutionary theory for further study of the species. This framework should be adequate for integrating the work that must be undertaken to achieve yet another more advanced level of understanding: details about distribution, in terms of ecological features, such as: altitudinal range and association with forest types; activity patterns and other aspects of life history; and geographical range, particularly in relation to the postulated areas of precinction (too many species of *Onypterygia* are known from single localities only). Additional character systems ought to prove enlightening: setal patterns and other aspects of larvae and pupae, and molecular data. We hope that this contribution, in the light of the additional knowledge required, will be seen as a step forward by those who follow us, in relation to the level of understanding that was achieved by those whom we have followed.

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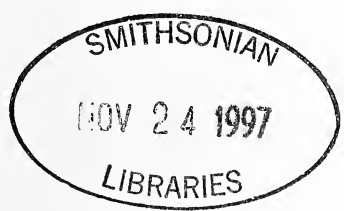
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HYBRIDIZATION AND SPECIATION IN *HYALOPHORA*
(INSECTA: LEPIDOPTERA: SATURNIIDAE):
A REAPPRAISAL OF W. R. SWEADNER'S CLASSIC
STUDY OF A HYBRID ZONE

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ABSTRACT

The historical significance of W. R. Sweadner's (1937) classic study of natural hybridization in *Hyalophora* is discussed in terms of contemporary and modern species concepts. Sweadner proposed that *Hyalophora* "kasloensis," from the Bitterroot Mountains of the Pacific Northwest, represents a natural hybrid population. In this monograph I re-examine his thesis using experimental hybridization and multivariate analysis, with laboratory hybrids serving as standards of reference. The ecology and immature stages of "kasloensis" are described. Biogeographical data, morphology of immature stages, morphometric data, and genetic compatibility in crosses with congeners all independently support the thesis that "kasloensis" populations are of hybrid origin. Two other newly discovered hybrid *Hyalophora* populations from the Pacific Northwest are described. Natural hybridization in *Hyalophora* is discussed in terms of various hybrid zone models. The genus *Hyalophora* represents a hierarchy of species, lacking effective prezygotic isolation, but exhibiting varying degrees of postzygotic barriers.

INTRODUCTION

Nature is lavish in her provision and wasteful in her economy. It is often difficult to tell where her reckless generosity ends and where the delicate limitations for the good of the species begins; in how far the individual shapes the race, or how far natural selection or other agencies eliminate the individuals in unnoticed millions in order to make the species the unit.

From Rau and Rau (1913:245) in introducing their study of fertility and embryo mortality in *Hyalophora cecropia*.

The Monograph by Sweadner

In 1937 Walter R. Sweadner published a monograph on the genus *Hyalophora* Duncan (= *Platysamia*; Lepidoptera: Saturniidae) in which he proposed natural hybridization as the basis for an intergrade population in the Bitterroot Mountains of the Pacific Northwest. He also advocated experimental hybridization as a tool in establishing phylogenetic relationships. This classic monograph appears to be the first comprehensive study published in English of a hybrid zone, a decade after the German classic by Meise (1928), and was the first to use a hybrid index to quantify phenotypic variation. Evolutionary biologists (Dobzhansky, 1951; Mayr, 1963; Dillon, 1973) cited Sweadner's monograph, both for its methods of investigation and for its modern views of the nature of species. However, in the intervening years few people have collected or reared the *Hyalophora* from the Bitterroot region, and the taxonomic status of these supposed hybrid populations

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Submitted 23 June 1995.

was uncertain. The name *kasloensis* was placed in synonymy with *H. euryalus* by Ferguson (1972) as a dark northern form of this West Coast species.

Evolutionary Genetics in the 1930s

Sweadner wrote and published his hybrid zone paper during an auspicious time in the development of evolutionary theory, punctuated by the publication of key concepts in genetics and systematics. Unfortunately, he drafted his manuscript just before Dobzhansky's (1937) synthesis of these disciplines in the first edition of "Genetics and the Origin of Species." Darwin's concept of gradual evolution in response to natural selection had earlier fallen into a kind of disrepute (Edey and Johanson, 1989), due largely to the work begun by T. H. Morgan in about 1911 and continued by Hermann Muller from the 1920s into the 1950s, using mutations as chromosome markers in *Drosophila*. Such mutations produced sudden, discrete, and often dramatic phenotypic change, which these workers proposed as a more likely mechanism of evolutionary change.

During this period, Fisher (1930) and Haldane (1932) developed a mathematical theory of gene frequency change in interbreeding populations subject to the effects of natural selection. To this body of population genetics theory, Wright (1932) contributed the role of inbreeding and the effect of genetic drift in small populations. Systematists of the time, including Sweadner, were confounded by the contrast between the geographic variation they observed in nature—often subtle, gradual, and clinal—and the abrupt and dramatic variation seen in the *Drosophila* laboratories. The newly formulated mathematics of population genetics offered little practical insight into the mechanism of speciation and evolution, partly because these abstract concepts of genes and alleles were difficult to relate to the complex characters systematists studied in the field and using museum specimens. The chemical structure of DNA, the fundamentals of transcription and of protein synthesis, and other basic aspects of gene expression were yet to be discovered. While the new genetic concepts strengthened Darwinism by providing a genetic basis for the origin of adaptations, they did not deal with the areas of weakness in Darwinian theory: the genetic changes that occur during speciation, and the properties that allow species to maintain their integrity in sympatry.

Dobzhansky (1937) combined the important elements of population genetics, the genetic and phenotypic variation seen in the field, and the genetic differences between species (largely from laboratory breeding of *Drosophila*) into the first modern synthesis of evolutionary thought (Coyne, 1994). Dobzhansky (1937) described speciation in terms of the origin of reproductive isolation, but since this work appeared the same year as Sweadner's (1937) monograph on the *Platysamia*, Sweadner was denied this insight into the genetics of speciation. Ironically, subsequent editions of Dobzhansky's book cited Sweadner's paper as an example of introgressive hybridization, the first step in the origin of species before the appearance of effective reproductive isolation.

Sweadner's Work and Subsequent Studies of Hyalophora

Breeding studies dating back to the turn of the century (Morton, 1895; Soule, 1902) showed that the members of the genus *Hyalophora* (which includes the familiar cecropia moth) lack effective mating barriers, and interspecific hybrids could be produced easily in captivity. Reared female hybrids are typically barren, but F₁ male hybrids are usually fully fertile and can be backcrossed to either

parent species. Sweadner (1934) conducted such studies using stock of *H. cecropia*, *H. columbia gloveri*, and *H. euryalus* and found that females of these species readily mated with males of any other species in captivity, and that tethered females would attract and mate with wild males of other species in a natural setting. Given the lack of mating barriers, it seemed likely that extensive hybridization would occur wherever the ranges of any two *Hyalophora* overlap. Even if hybrid females were barren, backcrossing by male hybrids might lead to intergradation between the forms in this region of initial hybridization.

A population of *Hyalophora* from the vicinity of Kaslo, British Columbia, had been described by Cockerell (1914) as *Samia rubra kasloensis*. Examination of specimens by Sweadner suggested to him that phenotypic variation in "*kasloensis*" might represent hybrid intergradation between the West Coast species *H. euryalus* (= *S. rubra*) and the Rocky Mountain species *H. gloveri*. Subsequent authors now consider the latter a subspecies of *Hyalophora columbia* (Collins, 1973; Kohalmy and Moens, 1975, 1988; Lemaire, 1978; Tuskes et al., 1996). In this paper I refer to populations of *Hyalophora* in the Bitterroot region simply by the name *kasloensis*, without quotes, as a convenience in communication and not in a formal taxonomic sense.

During a survey trip in 1932 to the Bitterroot Mountains of Idaho and Montana, Sweadner used a trap line of tied *Hyalophora* females to obtain samples along a transect from near Helena, Montana, west over Lookout Pass to Coeur d'Alene, Idaho. These locales appeared to represent the termini of a complete intergradation between the parent species. Using graphs and charts of wing character measurements, Sweadner (1937) represented this intergradation in what is one of the first uses of a hybrid index. Although Sweadner obtained 61 hybrid pairings, the difficulty of transcontinental travel prevented him from rearing larvae and conducting an extensive program of experimental hybridization. He was able to match laboratory *H. columbia gloveri* \times *H. euryalus* hybrids with wild specimens to further substantiate his theory of the origin of *kasloensis* through natural hybridization, which he proposed occurred as the result of postglacial range extensions from Ice Age refugia.

Sweadner made a second survey to investigate the possibility of natural hybridization between *H. cecropia* and the subspecies of *H. columbia*. The small, dark form *H. c. columbia* and *H. cecropia* are sympatric in the region of the Great Lakes; *H. cecropia* also contacts the larger, brighter form *H. columbia gloveri* along the eastern escarpment of the northern Rocky Mountains and in the prairies of Manitoba. Neither Sweadner (1937) nor Collins (1973) discovered evidence of extensive intergradation.

In his concluding remarks, Sweadner (1937:221) included a synopsis of contemporary species concepts and presented surprisingly modern insights provided by *Hyalophora* concerning the process of speciation. He interpreted the lack of complete reproductive isolation among the *Hyalophora* as an example of the gradual nature of speciation and of discordance in rates of evolution of various characters. In discussing the limitations of morphological criteria, such as genitalia in Lepidoptera, he stated: "Another system is the conception of Rassenkreise or Formenkreise in which the various local races. . . are placed together in a sort of a super species. The basis of differentiation is the tendency to pair." Here he presages Dobzhansky's (1937) use of reproductive isolation as a species criterion, but then states: ". . . the genus [*Hyalophora*] would make an excellent Formenkreise, but the female hybrids are all sterile, and the continuance of the hybrid

race [is] dependent on backcrossing to the parent species by the males." This problem of female barrenness, as seen in lab crosses, troubled Sweadner, who did not realize that females with normal fecundity can occur within hybrid zones.

By uniformly characterizing taxa, Sweadner was somewhat typological in his thinking, but at this time population genetics was not a part of traditional systematics and taxonomy. Nevertheless, he did recognize that different classes of traits may evolve at different rates: "Often two forms may be morphologically distinct but physiologically alike. . . . These forms or subspecies freely interbreed and produce fertile offspring. Usually physiological differentiation lags behind morphological differentiation." In his conclusion he remarks that "The genus *Platysamia* [= *Hyalophora*]. . . illustrate[s] the futility of attempting to set up rigid universal criteria for defining the limits of species."

Hybrid Zones in Studies of Speciation

The potential of hybrid zones to reveal evolutionary processes, only now being realized by evolutionary biologists, lured Sweadner into undertaking a challenging, even dangerous, cross-continental trek in the 1930s. Decades later, early students of hybrid zones (Sibley, 1954; Short, 1969) interpreted them as examples of the continuous and gradual nature of speciation. Under this interpretation, allopatric populations were assumed to have diverged in morphological and other characteristics, but to have lacked effective reproductive barriers; upon secondary contact the two taxa freely interbred, establishing a population of hybrids, identified by traditional morphological criteria. It was thought that hybrids were somehow unfit, due to low viability, sterility, or disruption of ecological adaptations, but few studies involved experimental breeding to test these ideas. Hybridization in nature between distinct taxa challenged the biological species concept based strictly on reproductive isolation. The disruption of "coadapted gene complexes" in hybrid genomes was thought to provide the basis in natural selection for the perfection of incipient reproductive isolation (Dobzhansky, 1951, 1971). On these grounds, hybrid zones were considered to be transitory phenomena.

Bigelow (1965) offered a descriptive model arguing against the origin of reproductive isolation in hybrid zones, thus partly explaining their stability. When hybrid unfitness is severe, the very condition thought to favor the origin of anti-hybridization mechanisms, Bigelow's (1965) model predicted that the barrier to introgression of foreign genes between species across the zone would be greater. Most matings just outside the zone will be between individuals with pure parental genotypes, and therefore these populations would not be subject to selection to prevent hybridization. Moreover, any change in mating behavior or physiology likely would be selected against in the parental populations as it would disrupt homospecific mating.

Slatkin (1973) and Endler (1977) discussed hybrid zones in terms of cline theory, in which they used computer models to examine the effect of varying rates of gene flow on gene frequencies for a single locus under selection by an environmental factor. In their models: (1) a gradient in selection intensity can produce a corresponding cline in the frequency of such genes, even in the face of gene flow; and (2) sharp clines form under conditions of strong selection and low dispersal, whereas gradual clines form where selection is weak and gene flow rates are higher. Under these conditions, reproductive isolation can evolve if linkage occurred between a gene under strong selection and a locus controlling critical

mating traits, a process termed parapatric speciation. These theoretical studies served as an admonition to critically re-examine the common assumption in hybrid zone studies of secondary contact after divergence in allopatry.

By the early 1980s, enzyme electrophoresis and other techniques in molecular genetics, combined with multivariate morphometrics, had spawned a new generation of hybrid zone studies. This empirical research inspired population geneticists to formulate detailed computer models of hybrid zones. Such models typically used cline theory and diffusion equations to predict the effects of selection and dispersal on gene exchange and introgression (Moore, 1977; Barton and Hewitt, 1981, 1985, 1989). The narrow width of hybrid zones, bounded by sharp phenotypic boundaries, were thought to reflect an equilibrium between dispersal, tending to broaden the zone, and selection against unfit recombinant genotypes, tending to narrow the zone of intergradation.

Hybrid zones are now seen as productive natural laboratories in studies of speciation (Hewitt, 1988, 1989, 1993; Harrison, 1990, 1993; Collins, 1991). The genetic similarity of hybridizing taxa, and the degree of genetic introgression across hybrid zones, can be estimated directly from allozyme and sequencing data. When estimates of dispersal rates are available, the shapes of clines can reveal the relative strength of selection on given alleles. Data collected on reproductive isolation relate directly to the process of speciation. Prezygotic isolation can be observed in the field, and can be studied in the lab for those organisms amenable to experimental manipulation. An understanding of postzygotic isolation and overall developmental genetic compatibility must be derived from laboratory hybridization and the rearing of experimental broods. The historical factors surrounding the origin of hybrid zones are the most difficult to determine (Harrison, 1990).

Collins (1984) analyzed a population of hybrids between *H. euryalus* and *H. columbia gloveri* near Lake Tahoe in the California Sierra Nevada Mountains. This population exhibited a great deal of phenotypic variation, exceeding that seen in reared primary hybrids, suggesting extensive backcrossing and genetic recombination. Female intergrades were fully fecund, unlike barren hybrid females produced by crossing allopatric stocks of *H. euryalus* and *H. c. gloveri*. With this work as background, in this paper I re-examine Sweadner's (1937) proposed hybrid origin for these Bitterroot populations of *Hyalophora*. Laboratory F₁ hybrids of known parentage served as reference standards in comparison with wild-collected and reared stock in experimental hybridization and multivariate morphometric analyses. The results of experimental hybridization are considered with respect to the taxonomy of intergrade populations in the Northwest and an interpretation of the phylogeny and patterns of speciation in the genus. The origin of hybrid zones is discussed in terms of current concepts of Pleistocene and postglacial biogeography.

METHODS AND MATERIALS

Collecting and Rearing Livestock

Wild males for use in discriminant analysis and for breeding stock were collected using funnel traps baited with a virgin *Hyalophora* female confined in a small cage above the funnel opening. Males responding to the "calling" female persistently fluttered about the vicinity of the small cage, and upon touching the smooth metal funnel usually slid through its opening. This type of moth trap has proven very effective for many species of saturniids (Collins and Weast, 1961; Collins, 1974, 1984). While Sweadner was able to tie out only single females along a trap line, a series of such funnel traps can obtain large samples over a wide area in a few days. All western taxa and populations of *Hyalophora*

emit pheromone from about 0300 hours until dawn (Sweadner, 1937; Collins, 1984). The genus is entirely univoltine and adults emerge in a concentrated flight period in late spring and early summer. Following a few preliminary field trips, I extensively trapped moths during late May and early June from 1989 through 1995 throughout Idaho and eastern Montana.

Females of native *Hyalophora* were collected at ultraviolet light traps, and occasionally at outdoor commercial lights. Such females usually have laid most of their ova, but often contain enough ova to start laboratory colonies. While no larvae or live cocoons of *kasloensis* were collected, immatures of *H. euryalus* and *H. c. gloveri* were collected in California, and reared stock of *H. c. gloveri* from Utah and of *H. c. columbia* from Ontario were obtained from local collectors.

Matings for specific experimental broods were obtained by confining males and females in nylon mesh cages or by enclosing a virgin female in the screen cage below the trap funnel, where she mated with a wild male after he entered the trap. Adult saturniids do not feed, and eclose with their entire complement of mature ova. Mated *Hyalophora* females readily oviposited in paper bags in the absence of a host plant. After oviposition was complete, usually after three to four days, ova were stored by cutting the paper bag into small pieces which were placed in plastic petri dishes, and stored at room temperature. The fecundity of a female was determined simply by counting the total number of ova laid; rarely, examination showed that a female still contained a significant number of ova, and these were dissected out and counted.

Unless otherwise noted, listed fecundity rates reflect the number of ova actually laid. After four or five days, infertile ova usually collapse, and infertility can be estimated reliably by counting these distorted ova. Most embryos that fail to hatch had attained nearly full development; the egg turns dark as normally occurs just prior to hatching, but the ovum does not collapse. An estimate of developmental genetic incompatibility is obtained easily by counting such unhatched ova, and in doubtful cases the ova can be dissected and examined under low magnification. Some errors occur where early embryo death is confused with infertility, but by these methods great numbers of ova (about 200 per female on average) were scored for female fecundity, percent fertile, and percent viable (hatched/fertile). Compatibility data were analyzed using pairwise Student's *t*-tests (BMDP-3D two-group test; Dixon, 1992) on arcsin-transformed percentages. Interpopulation crosses for *H. euryalus* and *H. c. gloveri* (Collins, 1984) were used for comparison. For analysis of fecundity, forewing length was chosen instead of weight to compensate for individual size variation because a large portion of the mass of a gravid female is ova whereas sterile hybrid females may be large but lack ova.

Larvae were reared by stapling a piece of paper containing typically 20 ova to a leaf of a host plant, and covering the branch with a strong, nylon mesh bag. Lots were divided up as larvae matured, and larvae were transferred to fresh foliage by cutting the twig or branch to which they were attached. Cocoons were collected after larvae spun in the bag. The great majority of larvae were reared on *Prunus emarginata* (bitter cherry) at about 1700 m in Nevada County, California. This host was accepted readily by all broods, produced large, healthy larvae, and is a known natural host for native *Hyalophora* throughout much of the western United States (Collins, 1984). Survival was typically 80% or more, although occasionally mice or vespid wasps were able to enter the sleeves. To assess the suitability of several other host plants, some broods were reared at lower elevation on various *Ceanothus* (Rhamnaceae) and other hosts, and others were sleeved on *Salix exigua* (coyote willow) along streams in Mono County, California. Cocoons were stored at 4°C in a refrigerator, and subsequently were incubated in screen cages in an outdoor insectary. By storing newly emerged, virgin females at high humidity in a refrigerator or ice chest, their normal life span of a week to ten days could be extended greatly, and a reliable supply of females could be taken into the field for use in traps and as mating stock. Collected males could be stored similarly for mating or until they could be spread. Accounts of life history and descriptions of immature stages are based on data acquired while collecting adults and rearing experimental broods.

Collecting localities for specimens used in discriminant analysis and for stock in experimental hybridization were as follows: **Montana:** Bearmouth, Granite County, 33 mi E Missoula, 3800 ft; Lolo Hot Springs, Missoula County, 7 mi E Lolo Pass, 4200 ft; 7 mi E Milltown, Missoula County, 3300 ft; Rock Creek, Missoula County, 22 mi E Missoula, 3750 ft; Sula, Spring Gulch campground, Ravalli County, 4420 ft. **Idaho:** Atlanta, Elmore County, 5600 ft; Gibbonsville, Lemhi County, 32 mi N Salmon, 4290 ft; Wild Goose campground, Idaho County, 20 mi E Kooskia, 1720 ft; intergrade population, NE of Boise: a transect from Idaho City–Mores Creek Summit–Clear Creek Canyon–Lowman (Helende and Bonneville campgrounds) to Banner Summit; Wallace to Kellogg, Shoshone County, 2700 ft. **California:** Banner Mountain, 5 mi E Nevada City, Nevada County, 3000 ft; Mulholland Canyon, Los Angeles County; Nevada County, 17 mi E Nevada City, 5000 ft Hwy 20; W of Donner Lake, Nevada County, 6200 ft; E slope Monitor Pass, Mono County, 6000–7250 ft; Panamint Mountains, Thorndike campground, Inyo County, 7500 ft; Big Pine Canyon, Inyo County, 7850 ft. **Nevada:** E Humboldt Range, Elko County. Oregon: 10 mi N Burns, Harney County, 4000 ft.

Discriminant Analysis

The principles and application of discriminant analysis in systematics are well known (Bookstein et al., 1985). Populations used as reference samples were selected based on their geographic proximity to suspected hybrid zones. Each reference sample was far enough removed from areas of intergradation to ensure that gene flow did not influence adult phenotypes. The *H. euryalus* reference sample was composed of specimens from northern California counties bordering Oregon. The reference sample for *H. columbia gloveri* included males from Boulder, Larimer, and Routt counties, Colorado. F_1 hybrids were made using *H. euryalus* females from Alpine County, California, and male *H. c. gloveri* from western Nevada. In addition to the reference samples and wild-collected adults, I was able to borrow the entire *Hyalophora* collection amassed by W. R. Sweadner, including wild material and reared specimens, from the Carnegie Museum of Natural History.

Wing characters and methods of measurement and scoring were modified from Collins (1984). Initially, a suite of 24 characters was submitted for stepwise discriminant analysis (program 7M, BMDP Statistical Software, Inc.; Dixon and Brown, 1990). These characters included both quantitative characters (e.g., wing length and eyespot length) and numerically scored qualitative characters (e.g., color of postmedial band). Initial analysis showed that six characters produced a discriminant function that correctly identified the three reference groups: ratio of length/width hindwing discal spot ($F = 189.30$, $df = 2$, 106); color forewing postmedial band ($F = 93.62$, $df = 4$, 210); presence/absence hindwing discal spot touching postmedial line ($F = 83.85$, $df = 6$, 208); shape of forewing basal band ($F = 74.05$, $df = 8$, 206); color ventral forewing band ($F = 64.73$, $df = 10$, 204); forewing length ($F = 58.41$, $df = 12$, 202).

Each individual was assigned to one of the reference groups: *H. euryalus*, *H. c. gloveri*, or their F_1 hybrid. By analyzing the frequency distribution of distance values for each reference group, I determined criteria to assign an individual specimen to one of five classes, where classes 2 and 4 represent an intermediate position between *H. euryalus* and the F_1 hybrids, or between *H. c. gloveri* and the hybrids, respectively. Experience from the Sierra Nevada study had shown that many hybrid zone specimens fell into these classes, roughly corresponding to backcross individuals.

I had intended to rescore Sweadner's intergrade specimens and compare my discriminant classifications to his phenotype scores. Unfortunately, while Sweadner's original data labels and code numbers remain affixed to most specimens, no field or lab notebooks were found containing the character scores for any of his specimens, precluding these comparisons.

RESULTS

Genetic Compatibility

Hatch rate for interpopulation matings among *kasloensis* broods ranked lower than those for pure *H. euryalus* or *H. c. gloveri*, reciprocal F_1 crosses with these species, or even those for *kasloensis* \times *H. c. columbia* or *H. euryalus* \times *kasloensis* matings; this ranking was obtained also for "non-sib" *kasloensis* matings (Table 1). Of the 15 groups, the eight crosses with lowest index (percent hatched per ova laid) values involved *kasloensis* (Table 2). Data supplied by Dean Morewood (personal communication) also showed a degree of incompatibility between *H. euryalus* from the vicinity of Victoria, British Columbia, and *kasloensis* from the Okanagan Valley, interior British Columbia (Table 1).

Fertility in interpopulation crosses within *H. euryalus* is significantly higher than in test crosses within *H. c. gloveri*, although the source populations of *H. c. gloveri* were as widely separated as Utah and California (Table 3). All crosses of *H. euryalus* were from within California, except for two crosses with stock from Victoria, British Columbia (\times male, Nevada County, California = 96.9%; \times female, Los Angeles County, California = 81.1%). Viability rates were not significantly different for *H. c. gloveri* vs. *H. euryalus* (Table 4).

Using interpopulation matings for *H. c. gloveri* as a conservative standard, the fertility rate for pooled *kasloensis* ranked significantly lower, but non-sib matings for *kasloensis* did not differ significantly ($P = 0.29$; Table 3). Pooled reciprocal F_1 crosses between *H. euryalus* and *H. c. gloveri* also had significantly higher

Table 1.—*Compatibility indices in experimental crosses (female × male) between Hyalophora “kasloensis” and congeners: fecundity (number of ova laid), fertility (percentage of ova laid that were fertile), and viability (percentage of fertile ova that hatched), (N) = number crosses for pooled data.*

Group, cross	Fecundity	Fertility	Viability
I. Intrapopulation <i>H. kasloensis</i>			
1. female to UV Lolo Hot Springs, Montana	57	94.7	98.2
2. progeny above × sib	117	100.0	85.8
3. progeny 1 × Milltown, Montana	107	80.8	81.0
4. progeny II-6 × Sula, Montana	142	66.7	100.0
5. progeny II-6 × sib	168	64.6	67.7
6. progeny 5 × progeny 4	155	40.2	81.4
7. progeny 5 × sib	168	80.4	61.1
		75.3	82.2
II. Interpopulation <i>H. kasloensis</i>			
1. Lolo Hot Springs × Sula	106	66.7	79.5
2. Lolo Hot Springs × Wild Goose Campground, Idaho County, Idaho ¹	158	93.8	100.0
3. progeny 1 × Sula	140	90.8	92.8
4. progeny 1 × progeny I-3	181	99.4	95.6
5. progeny 1 × sib	168	81.0	95.0
6. progeny II-4 × progeny 3	133	80.4	91.0
7. progeny 6 × Wallace, Idaho	177	99.2	96.7
8. as above	125	84.4	98.7
		87.0	93.7
Pooled <i>H. kasloensis</i> nonsib matings (10)		85.7	93.4
Pooled <i>H. kasloensis</i> sib matings (5)		73.2	78.2
Data from D. Morewood (personal communication):			
1. Okanagan Valley, British Columbia, Canada × same	239	95.4 hatched/laid	
III. <i>H. euryalus</i> × <i>H. kasloensis</i>			
1. Banner Mountain, Nevada County, California × Lolo Hot Springs	180	92.8	100.0
2. Donner Lake, Nevada County, California × west Lolo Hot Springs	171	76.7	95.3
3. Banner Mountain × Bearmouth, Montana	164	92.1	99.3
4. Banner Mountain × Milltown, Montana	148	93.2	99.3
5. as above	102	0 ²	0
		88.7	98.5
IV. <i>H. kasloensis</i> × <i>H. euryalus</i>			
1. progeny II-2 × Banner Mountain (female small)	92	80.4	0
2. progeny II-2 × Nevada County, California (female small)	30	96.7	100.0
3. progeny I-1 × Nevada County	130	98.4	100.0
4. progeny II-1 × Banner Mountain	170	99.4	100.0
5. progeny I-2 × Banner Mountain	188	85.0	96.9
6. progeny I-3 × Banner Mountain	171	90.1	98.7
7. progeny II-5 × Burns, Oregon	122	82.0	99.0
		90.3	84.9
Data provided by D. Morewood (personal communication):			
1. Okanagan Falls, British Columbia, Canada × Victoria, British Columbia, Canada	69	69.6 hatched/laid	
2. as above	95	80.0 hatched/laid	
3. as above	106	90.6 hatched/laid	

Table 1.—Continued.

Group, cross	Fecundity	Fertility	Viability
V. F ₁ hybrid (<i>H. euryalus</i> × <i>H. kasloensis</i>)			
1. (progeny III-3) × Gibbonsville, Idaho <i>gloveri</i>	164	77.5	96.8
2. as above	176	79.2	100.0
		78.4	98.4
3. as above × Nevada County <i>euryalus</i>	54	87.0	74.5
4. (Banner × Bearmouth) × Banner Mountain <i>euryalus</i> (retained 65 ova; 97 total)	32	88.9	68.8
5. (Banner × Milltown) × Nevada County <i>euryalus</i>	131	71.4	97.8
		82.4	80.4
6. (Banner × Milltown) × progeny II-3 <i>kasloensis</i>	108	93.5	91.1
		82.9	88.2
VI. F ₁ hybrid (<i>H. kasloensis</i> × <i>H. euryalus</i>)			
1. progeny IV-2 × Banner Mountain <i>euryalus</i>	62	93.4	100.0
2. as above	59	96.6	98.3
		95.0	99.2
3. progeny IV-3 × <i>kasloensis</i> progeny II-5	130	37.1	87.0
VII. <i>H. c. gloveri</i> × <i>H. kasloensis</i>			
1. California: [(Monitor Pass-Big Pine) × Big Pine] × Wild Goose	123	65.9	50.6
2. as above × 3 mi east Lolo Hot Springs	184	47.8	48.9
3. (Monitor Pass) × Rock Creek, Montana	176	77.3	78.7
4. (Walker River × Monitor Pass) × 3 mi east Milltown	175	0 ²	0
5. Walker River × progeny II-1	276	99.0	100.0
6. Walker River × progeny I-4	184	92.4	97.1
		76.5	75.1
VIII. <i>H. kasloensis</i> × <i>H. c. gloveri</i>			
1. progeny II-1 × Gibbonsville	193	98.5	98.5
2. Lolo Hot Springs × Walker River	145	84.0	93.0
3. Lolo Hot Springs × Gibbonsville	163	69.3	94.9
4. as above	144	74.7	95.8
5. progeny II-6 × east Humboldt Range, Elko County, Nevada	173	74.2	97.8
		80.1	96.0
IX. F ₁ hybrid (<i>H. c. gloveri</i> × <i>H. kasloensis</i>)			
1. F ₁ (Monitor Pass × Rock Creek) × Lolo Pass <i>kasloensis</i>	94	89.6	98.8
2. <i>kasloensis</i> progeny II-5 × F ₁ progeny VII-5	69	37.1	87.0
3. as above	196	56.0	71.9
4. II-5 <i>kasloensis</i> × (<i>gloveri</i> × <i>kasloensis</i>) VII-5	69	37.1	76.9
5. as above	196	56.0	71.9
X. F ₁ hybrid (<i>H. kasloensis</i> × <i>H. c. gloveri</i>)			
1. F ₁ progeny VIII-1 × F ₁ progeny VIII-2	65	4.6	33.3
2. F ₁ progeny VIII-1 × progeny II-3 <i>kasloensis</i>	0		
3. as above	2	0	0
4. progeny VIII-3 × progeny II-4 <i>kasloensis</i>	1	0	0
5. progeny VIII-1 × Boise County, Idaho hybrid zone	40	10.0	100.0
XI. <i>H. c. columbia</i> × <i>H. kasloensis</i>			
1. <i>columbia</i> Ontario, Canada × Sula	134	75.5	98.2
2. (<i>c. columbia</i> Ontario, Canada × <i>gloveri</i> Panamint Mts., California) × Milltown, Montana	236	88.5	97.9

Table 1.—Continued.

Group, cross	Fecundity	Fertility	Viability
3. <i>c. columbia</i> Ontario, Canada × progeny II-1	126	49.2	62.9
		71.7	86.3
XII. <i>H. kasloensis</i> × <i>H. c. columbia</i>			
1. Lolo Hot Springs × <i>columbia</i> Ontario, Canada	127	95.2	96.0
XIII. F ₁ hybrid (<i>H. c. columbia</i> × <i>H. kasloensis</i>)			
1. progeny XI-3 × progeny II-4 <i>kasloensis</i>	143	92.3	72.0
2. as above	37	66.7	43.8
3. progeny XI-1 × <i>kasloensis</i> Sula	117	34.4	45.2
4. progeny I-2 <i>kasloensis</i> × progeny XI-1 F ₁ : infertile mating, ♀ retained ova			
5. progeny XI-1 × <i>c. columbia</i>	0		
6. progeny XI-1 × <i>gloveri</i> east Humboldt Range, Nevada	121	77.4	100.0
7. progeny 6 × <i>gloveri</i> Denver, Colorado	99	46.5	87.0
8. (F ₁ <i>kasloensis</i> × <i>c. columbia</i>) × <i>c. columbia</i>	barren		
9. (as above) × <i>gloveri</i>	barren		
XIV. <i>H. kasloensis</i> × Boise County, Idaho, intergrade population			
1. progeny II-1 × Helende Campground	109	95.4	95.2
2. progeny II-6 × 9 mi east Idaho City	210	92.6	94.0
3. progeny II-5 × Lowman	131	18.4	100.0
		68.8	96.4
XV. <i>H. euryalus</i> × Boise County, Idaho, intergrade population			
1. Mulholland × Helende	175	100.0	100.0
2. Mulholland × Bonneville Campground	127	97.6	100.0
3. Banner Mountain × 10 mi north Idaho City	145	89.7	99.2
4. as above	187	92.8	100.0
		95.0	99.8
XVI. F ₁ (<i>H. euryalus</i> × <i>H. kasloensis</i>) × Boise County, Idaho, intergrade population			
1. (Banner Mountain × Milltown) × Lowman	121	80.0	92.7
2. progeny above × Clear Creek Canyon	206	100.0	99.5
3. as above	162	97.2	98.6
4. progeny 2 (old female) × Clear Creek Canyon	157	40.1	98.4
5. progeny 2 (old) × Boise River <i>gloveri</i>	169	61.6	99.0
6. progeny 5 × (3) Idaho City	151	58.3	98.4
XVII. <i>H. c. gloveri</i> × Boise County, Idaho, intergrade population			
1. (Walker River × sib) × Atlanta, Idaho	277	91.9	80.1
2. (Utah × sib) × Clear Creek Canyon	214	98.1	100.0
3. (Utah × sib) × Clear Creek Canyon	200	98.1	99.4
		96.0	93.2
XVIII. Reference crosses, pooled data ³			
1. interpopulation <i>H. euryalus</i> (15)	213.5	97.0	98.7
2. interpopulation <i>H. c. gloveri</i> (8)	215.3	91.5	99.5
3. <i>H. c. gloveri</i> × <i>H. euryalus</i> (8)	255.7	91.7	98.0
4. <i>H. euryalus</i> × <i>H. c. gloveri</i> (9)	197.1	91.2	96.9
5. <i>H. c. columbia</i> × <i>H. euryalus</i> (3)	131.7	71.9	93.1

¹ Due to holdover pupae in diapause, sibs of parental broods in some cases were mated to progeny of these parental broods.

² Note: "0" values for fertility not entered in calculation of mean values.

³ From Collins, 1984.

Table 2.—Summary of genetic compatibility for *Hyalophora* (n, number of matings), arranged by decreasing index values: fertility (percent fertile of ova laid), viability (percent of fertile ova that hatched), and index (percent of ova laid that hatched).

Origin, female × male (n)	Fertility	Viability	Index
Interpopulation <i>H. euryalus</i> (15)	97.0	98.7	95.7
<i>H. euryalus</i> × Boise, Idaho, Hybrid Zone (4)	95.0	99.8	94.8
<i>H. kasloensis</i> × <i>H. c. columbia</i> (1)	95.2	96.0	91.4
Interpopulation <i>H. c. gloveri</i> (8)	90.7	99.5	90.3
<i>H. c. gloveri</i> × <i>euryalus</i> (8)	91.7	98.0	89.9
<i>H. c. gloveri</i> × Boise, Idaho, Hybrid Zone (3)	96.0	93.3	89.5
<i>H. euryalus</i> × <i>H. c. gloveri</i> (9)	91.2	96.9	88.4
<i>H. euryalus</i> × <i>H. kasloensis</i> (4)	88.7	98.5	87.4
Interpopulation <i>H. kasloensis</i> (8)	87.0	93.7	81.5
<i>H. kasloensis</i> non-sib pooled (10)	85.7	93.4	80.0
<i>H. kasloensis</i> × <i>H. c. gloveri</i> (5)	80.1	96.0	76.9
<i>H. kasloensis</i> × <i>H. euryalus</i> (7)	90.3	84.9	76.7
<i>H. kasloensis</i> × Boise, Idaho, Hybrid Zone (3)	68.8	96.4	66.3
<i>H. c. columbia</i> × <i>H. kasloensis</i> (3)	71.7	86.3	61.9
<i>H. c. gloveri</i> × <i>H. kasloensis</i> (5)	76.5	75.1	57.5

fertility rates than those for pooled *kasloensis*, but did not differ from those for non-sib *kasloensis* ($P = 0.21$).

Again using *H. c. gloveri* as a standard, variation in viability among all groups was not significant except for both pooled and non-sib *kasloensis* (Table 4). Using *H. euryalus* as a standard, significant differences were found for all crosses involving *kasloensis*, including those involving female *kasloensis* × male *H. euryalus*.

In comparisons of hatch rate, female *H. euryalus* were the most compatible in crosses with other taxa, although the number of replicates involving female *H. c. columbia* is low (Table 2). Both reciprocal crosses between *H. c. gloveri* and *H. euryalus* showed a higher hatch rate than the crosses involving *H. c. gloveri* with *kasloensis*.

Wild males from the hybrid zone near Boise, Idaho, were more compatible with females of pure *H. euryalus* and *H. c. gloveri* than either of these species were when crossed with male *kasloensis*. Also, two of the three crosses (Table 1: group XIV) between a female *kasloensis* and a male from the Boise hybrid zone resulted in an average hatch rate of 88.9% (not shown in Table 1), only slightly lower than that for crosses with female *H. c. gloveri*. The high genetic compatibility between males from this zone and females of other taxa contrasts with that of the *kasloensis* populations. This trend may result from more balanced gene introgression in the Boise hybrid zone, in contrast with the asymmetrical *kasloensis* zone (see below). Crosses between female *kasloensis* and male *H. c. gloveri* from the Gibbonsville location showed reduced fertility rates, as did other crosses with more distant populations of *H. c. gloveri*.

Natural populations, ranked in order of decreasing absolute fecundity and fecundity indices, are: *H. cecropia*, *H. c. gloveri*, *H. euryalus*, and *kasloensis* (Table 5). The fecundity for female *kasloensis* is low, even given their smaller average wing size. The fecundity of female *H. euryalus* × *kasloensis* hybrids is substantially lower than that of *kasloensis* but greater than those of other hybrid combinations. While the fecundity of *H. c. columbia* × *kasloensis* females is much lower than that for "pure" taxon broods, the fecundity of these hybrid females

Table 3.—Pairwise Student's *t*-tests (*df*) of arcsin-transformed fertility data for experimental broods of *Hyalophora*: statistic, probability. Reciprocal crosses pooled in some cases to increase sample sizes.

Group (n)	<i>euryalus</i>	<i>eury.</i> × <i>glov.</i> <i>glov.</i> × <i>eury.</i>	<i>kasloensis</i> pooled	Non-sib <i>kasloensis</i> (11)	<i>kaslo.</i> × <i>eury.</i> (7)	<i>glov.</i> × <i>kaslo.</i> <i>kaslo.</i> × <i>glov.</i> (10)
<i>H. c. gloveri</i> ¹ (8)	-2.74 (21)	-0.13 (23)	1.57 (19)	1.05 (17)	0.15 (13)	1.97 (16)
	0.012** ²	0.899	0.133	0.308	0.884	0.067*
<i>H. euryalus</i> ¹ (15)		2.689 (30)	4.11 (26)	3.76 (24)	2.57 (20)	4.62 (23)
		0.012**	0.0003***	0.001***	0.018**	0.0001***
<i>H. euryalus</i> × <i>H. c. gloveri</i> ¹ (17)			2.07 (28)	1.31 (26)	-0.26 (22)	2.43 (25)
<i>H. c. gloveri</i> × <i>H. euryalus</i>			0.047**	0.202	0.796	0.22**
<i>H. kasloensis</i> (13) pooled				-0.49 (22)	1.32 (18)	1.07 (21)
				0.0629	0.203	0.297

¹ Collins, 1984; unpubl.
² NS ($P > 0.10$), * ($0.05 < P < 0.10$), ** ($0.01 < P < 0.05$), *** ($P < 0.01$).

Table 4.—Pairwise Student's t-tests (df) of arcsin-transformed viability data for experimental broods of *Hyalophora*: statistic, probability. Reciprocal crosses pooled in some cases to increase sample sizes.

Group (n)	<i>euryalus</i>	<i>eury. × glov. glov. × eury.</i>	<i>kasloensis</i> pooled	Non-sib <i>kasloensis</i>	<i>kaslo. × eury.</i> (7)	<i>glov. × kaslo. kaslo. × glov.</i> (10)
<i>H. c. gloveri</i> ¹ (8)	0.51 (21)	1.51 (23)	3.59 (19)	2.93 (17)	1.16 (13)	2.75 (16)
<i>H. euryalus</i> ¹ (15)	0.614	0.145	0.002*** ²	0.009***	0.268	0.014**
		1.17 (30)	4.15 (26)	2.97 (24)	1.43 (20)	3.26 (23)
		0.252	0.0003***	0.007***	0.167	0.003***
<i>H. euryalus × H. c. gloveri</i> ¹ (17)			3.47 (28)	2.05 (26)	−1.18 (22)	2.75 (25)
<i>H. c. gloveri × H. euryalus</i>			0.002***	0.051*	0.249	0.011**
<i>H. kasloensis</i> (13) pooled					−0.03 (20)	1.06 (19)
					0.947 ³	0.304

¹ Collins, 1984; unpubl.
² NS ($P > 0.10$), * ($0.05 < P < 0.10$), ** ($0.01 < P < 0.05$), *** ($P < 0.01$).
³ Probability shown is interpopulation *kasloensis*; intrapopulation = 0.166.

Table 5.—Fecundity (number ova laid, mean \pm SD), mean length of forewing, and their ratio among *Hyalophora* species and their hybrids.

Group (n)	Fecundity	Forewing length	Fecundity/ forewing length
<i>H. cecropia</i> ¹	271.5 \pm 69.5	75.0	3.62
<i>H. euryalus</i> (12)	175.5 \pm 36.8	58.3 \pm 4.6	2.99 \pm 0.48
<i>H. c. columbia</i> (1)	134.0	55.0	2.44
<i>H. c. gloveri</i> (13)	221.1 \pm 45.2	62.9 \pm 4.2	3.52 \pm 0.74
<i>H. c. columbia</i> \times <i>H. c. gloveri</i> (4)	177.8	59.3	3.02
<i>H. kasloensis</i> (25)	149.6 \pm 32.1	55.8 \pm 2.3	2.62 \pm 0.50
F ₁ <i>H. euryalus</i> \times <i>H. kasloensis</i> (6)	132.8	56.8	2.32
F ₁ <i>H. c. columbia</i> \times <i>H. kasloensis</i> (4)	79.5	55.8	2.07
F ₁ <i>H. kasloensis</i> \times <i>H. c. gloveri</i> (5)	21.6	57.9	0.36
Monitor Pass, Mono County, California hybrid zone (bred intergrades) (5)	222.0	64.2	3.46

¹ Index calculated from separate averages for fecundity ($n = 32$) and forewing length (15).

exceeded that of hybrid females from *kasloensis* \times *H. c. gloveri* crosses; this pattern parallels that for hatch rate (Table 1). The fecundity of intergrade females from the Monitor Pass hybrid zone was comparable to that of pure *H. c. gloveri*. No data are available for females from the Boise hybrid zone. However, progeny from matings of wild Boise hybrid zone males with female (*H. euryalus* female \times *kasloensis* male) hybrids were successively crossed for three generations to wild males in the Boise hybrid population, and consistently yielded females with a high fecundity (Table 1: group XVI, cross 1). This result suggests that the Boise hybrid population contains fully fecund females, similar to females from both *kasloensis* and the Monitor Pass hybrid population.

Pure *kasloensis* crosses yielded a normal ratio of males to females (Table 6), as did experimental, reciprocal crosses between *H. euryalus* and *H. c. gloveri* (Collins, 1984). Distortion of the sex ratio occurred in crosses between female *kasloensis* and male *H. euryalus*, and also in crosses between female *H. c. gloveri* and male *kasloensis*. Although the female offspring from matings between female *H. euryalus* and male *kasloensis* had only slightly lowered fecundities (Table 5), the sex ratio was distorted in the backcross brood involving these F₁ females and a pure *H. euryalus* male (Table 6). In general, sex ratios indicate an incompatibility in at least some combinations involving *kasloensis* and either *H. euryalus* or *H. c. gloveri*. The sex ratio of progeny from crosses of female *H. c. columbia*

Table 6.—Deviation from 1:1 sex ratios in experimental hybrid broods for *Hyalophora*.

Cross (female \times male)	Number enclosed		Chi-square value ¹
	Female	Male	
<i>H. kasloensis</i>	44	40	0.190 ^{NS}
<i>H. euryalus</i> \times <i>H. kasloensis</i>	17	20	0.243 ^{NS}
<i>H. kasloensis</i> \times <i>H. euryalus</i>	19	32	3.314*
<i>H. c. gloveri</i> \times <i>H. kasloensis</i>	8	13	1.191 ^{NS}
<i>H. kasloensis</i> \times <i>H. c. gloveri</i>	16	15	0.032 ^{NS}
<i>H. c. columbia</i> \times <i>H. kasloensis</i>	13	11	0.167 ^{NS}
<i>H. kasloensis</i> \times <i>H. c. columbia</i>	1	3	NSD
F ₁ (<i>H. euryalus</i> \times <i>H. kasloensis</i>) \times <i>H. euryalus</i>	6	15	3.857**

¹ P-value: NS ($P > 0.10$), * ($0.01 < P < 0.05$), ** ($P < 0.01$); NSD = not sufficient data.

Table 7.—Compatibility indices in experimental crosses (female \times male) between *Hyalophora cecropia* and congeners: fecundity (number of ova laid), fertility (percentage of ova laid that were fertile), viability (percentage of fertile ova that hatched), hatch rate (percentage of ova laid that hatched).

Group Locality	Fecundity	Fertility	Viability	Hatch rate
Intrapopulation <i>H. cecropia</i>				
Urbana, Illinois, ¹ wild (11)	368.7			91.3
Urbana, Illinois, reared nonsib ¹ (4)	277.0			96.2
Urbana, Illinois, wild	326	99.1	61.3	60.7
Denver, Colorado, wild	284	98.9	94.7	93.7
St. Louis, Missouri (avg. 35 pairings) ²		85.5		77.0
Interpopulation <i>H. cecropia</i>				
Ohio, Hancock County \times Iowa, Polk County	382	99.2	100.0	99.2
<i>H. cecropia</i> \times <i>H. columbia gloveri</i>				
Madison, Wisconsin \times Gallatin County, Montana	337	53.3	96.7	51.5
Urbana, Illinois \times Salt Lake City, Utah ³	204			0
As above	355			89.3
As above	425			87.1
<i>H. columbia gloveri</i> \times <i>H. cecropia</i>				
Salt Lake City, Utah \times Urbana, Illinois ³	306			92.8
As above	190			85.8
As above	90			0
As above	228			90.8
As above five females: no ova laid				
<i>H. cecropia</i> \times <i>H. c. columbia</i> (see text)				
<i>H. cecropia</i> \times <i>H. euryalus</i>				
Illinois \times Monterey, California ³	292			55.1
As above	250			3.6
As above	265			1.1
Illinois \times Nevada County, California	259	100.0	99.6	99.6
Three matings as above, normal number ova laid, all infertile				
<i>H. euryalus</i> \times <i>H. cecropia</i>⁴				
Monterey, California \times Urbana, Illinois ³	200			71.0

¹ Waldbauer and Sternburg, 1979.

² Rau and Rau, 1913. Pedigree of stock not given, ova handled excessively.

³ Unpublished data supplied by J. Bruce Duncan. All other data from author's unpublished research.

⁴ This cross typically results in damage to the genitalia of the female *H. euryalus* by the claspers of the larger *H. cecropia* male (see text), preventing oviposition.

with male *kasloensis* was normal; too few progeny of the reciprocal cross were reared to test.

Available data indicate that the compatibility of *H. cecropia* with congeners is less than that between *H. euryalus* and *H. columbia gloveri* (Table 7). Fertility and viability are both normal in reciprocal crosses between the latter species (Table 1). Mechanical prezygotic isolation based on size difference and postzygotic genetic incompatibility is expressed in crosses between both *H. cecropia* and *H. c. columbia*, as well as in crosses between *H. cecropia* and *H. euryalus*. Tuttle (1985) found that captive *H. cecropia* typically resisted mating attempts of wild *H. c. columbia* males, or if cross-mated would re-mate conspecifically; oviposition rate and hatch rate were low in the few successful hybrid crosses. The large claspers of male *H. cecropia* physically damaged the genitalia of the smaller

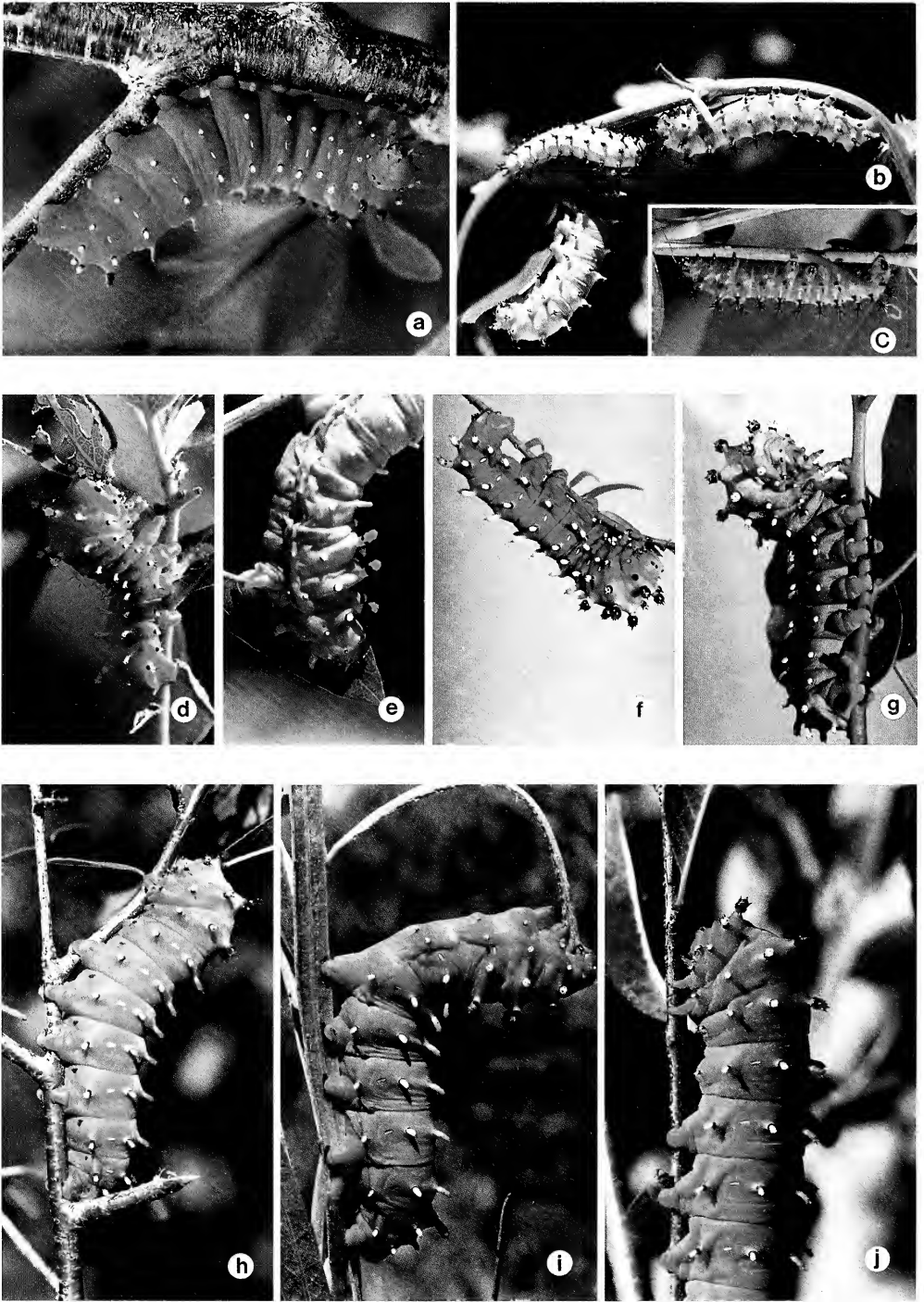


Fig. 1.—Larvae of *Hyalophora*. a–c, *H. "kasloensis,"* Lolo Hot Springs, Missoula County, Montana. a, fifth instar, $\times .75$; b, fourth instars, note variation in melanization of scoli, approx. $\times 1.0$; c, third

H. c. columbia female in other hybrid pairings, preventing oviposition. The hatch rate of crosses between female *H. cecropia* and male *H. euryalus* is low (Table 7), and the reciprocal cross usually resulted in damage to the genitalia of *H. euryalus* (Weast, 1959; Collins and Weast, 1961; Tuskes et al., 1996). More infertile matings appear to occur in crosses between *H. cecropia* and *H. euryalus* than between the former and *H. c. gloveri*.

Available data suggest that *H. cecropia* is somewhat more compatible with *H. c. gloveri* than with either *H. c. columbia* or *H. euryalus*. Females of *H. c. gloveri* are only slightly smaller on average than *H. cecropia*, and mechanical prezygotic isolation apparently does not occur. Yet very few natural hybrids have been collected where these two species are sympatric on the east slopes of the northern Rockies and in the Canadian Prairie Provinces (Tuskes et al., 1996). Reproductive isolation in the wild has not been studied to date.

Life History and Immature Stages of Hybrid Populations

No complete description of the immature stages of *kasloensis* has been published. Sweadner (1937) was unable to obtain live material of *kasloensis* and the immature stages were unknown to him. He noted that the final instar of various hybrid larvae with a male *kasloensis* as a parent differed from all other *Hyalophora* taxa in that all the dorsal scoli were reddish. All other forms have yellow dorsal abdominal scoli in the final instar (Tuskes et al., 1996). Morewood (1991) confirmed the presence of red scoli in a brief description of British Columbia stock of *kasloensis*, and he illustrated the last two instars. The larval phenotypes from the Bitterroot Mountains appear similar to his descriptions (Fig. 1). The following descriptions (measurements in mm) are based on stock obtained from wild females collected near Lolo Hot Springs and Sula, Montana, and from broods resulting from mating these progeny to wild males (Table 1).

Ova.—Oval, not noticeably tapered; slightly dished on one side in viable ovum. Length: \bar{x} = 2.34, range 2.10–2.55. Width: \bar{x} = 1.68, range 1.63–1.74. Attached to surfaces by a dark reddish-brown gum-like cement. Ova of *H. euryalus* slightly larger: 2.56×2.08 average.

First Instar.—Length 8–10 at rest at end of stadium. Head, legs, prolegs, and scoli deep, shiny black. Integument dull black, developing dull yellow around base of spiny scoli as larva grows. The first instar larvae of *H. c. gloveri*, *H. euryalus*, and *kasloensis* cannot be separated reliably by any combination of characters.

Second Instar.—Length 12–15. Head black, sometimes with yellow-green medially. All scoli shiny black. Body at first dull yellow, changing to yellow-green with areas of yellow surrounding base of scoli by mid-instar. Black, diamond-shaped or wedge-shaped marks medially between dorsal scoli of all segments. Intersegmental black markings expressed to varying degrees. The second instar

←

instar, $\times 1.25$. d, e, *H. euryalus*, Nevada County, California. d, fourth instar photographed in nature, $\times 1.0$; e, fifth instar, $\times .85$. f, *H. c. columbia* fifth instar, Michigan, Livingston County, $\times 1.0$. g, *H. columbia gloveri*, fifth instar, Utah, vicinity Salt Lake City, $\times 1$. h, *H. "kasloensis"* ♀ $\times H. c. columbia$ ♂, fifth instar, $\times .75$. i, *H. euryalus* ♀ $\times H. "kasloensis"$ ♂, fifth instar, $\times .80$. j, *H. "kasloensis"* ♀ $\times H. c. gloveri$ ♂, fifth instar, $\times 1.0$.

is also nearly identical to *H. c. gloveri*; most second instars of *H. euryalus* are somewhat brighter yellow, especially early in the stadium.

Third Instar.—Length 18–20. Head dull green with paired black marks tapering toward mouth. Body dull grey-green shading into yellow-green laterally, marked with small black dots ventrally. Prolegs and scoli black. The overall appearance is closer to *H. c. columbia*, which has black scoli in the third instar, than to *H. c. gloveri*, which may have orange dorsal scoli and blue lateral scoli, often black at tips. In this instar *H. euryalus* has bright yellow dorsal and light blue lateral scoli, with no tendency toward melanization. Some *H. euryalus* populations in extreme southern California and Baja California may have orange dorsal scoli.

Fourth Instar.—Length 33–38. Head and integument dull blue-green, shading to faint yellow tinge laterally and on prolegs. Dorsal thoracic and dorsal first abdominal scoli a deep coral red, encircled with black at base. In about one-half of larvae examined the dorsal abdominal scoli are red-orange to light orange, with light blue lateral scoli. Other larvae have all scoli black at tip, showing color only at base. Approximately one-fourth of larvae have all black lateral and dorsal scoli on all segments. Setae black in all color forms. This range of scoli color variation may be seen in one brood. A similar variation is seen in *H. c. gloveri*, which would be difficult to separate from *kasloensis*, except for a tendency to have somewhat stouter scoli with more prominent setae. Fourth instar *H. c. columbia* invariably has all scoli a deep, shiny black, and this phenotype is also identical to the corresponding variation in *kasloensis*. The fourth instar of *H. euryalus* has yellow dorsal scoli, and light blue lateral scoli, and never expresses the melanic variation seen in the subspecies of *columbia* or in *kasloensis*.

Fifth Instar.—Length 65–80. Head and integument dull green to dull blue-green, similar to *H. c. gloveri*. Dorsal thoracic scoli and dorsal scoli on first abdominal segment deep coral red. These three pairs of scoli encircled at base with a series of irregular black markings. Remaining dorsal abdominal scoli red to red-orange. Lateral scoli on all segments light blue, blue-white at tip, black at base. Both *H. c. gloveri* and *H. euryalus* have all dorsal scoli yellow. The enlarged dorsal thoracic scoli and dorsal first abdominal scoli in *H. euryalus* are encircled with a prominent black band of even width. This marking in *H. c. gloveri* and *H. c. columbia* is irregular, often in the form of blotches, just touching. The corresponding black marking in *kasloensis* is intermediate. The dorsal thoracic and first abdominal scoli in *H. c. columbia* are the same deep red as in *kasloensis*, the remaining dorsal abdominal scoli are yellow to pinkish-yellow. In *H. euryalus*, all scoli other than the dorsal thoracic are often more elongated than in other taxa, which have scoli of a more spherical or bulbous shape. In this regard, *kasloensis* resembles more closely the subspecies of *H. columbia*.

Cocoon.—All *Hyalophora* spin a double-walled cocoon with a loose intervening mesh. At one end is an eclosion valve, made up of strands spun parallel and tapering to a point. The cocoon of *H. c. gloveri* is compact and adorned with silvery or golden bands of silk. The cocoon is impregnated with a fluid which darkens the silk, except for the distinctive bands. These cocoons are dull brown to grey, and in color and texture resemble bark and dried leaves. The larvae of *H. c. gloveri* usually spin at the base of the host or in nearby dense vegetation. The northern subspecies *H. c. columbia* spins a smaller, darker, and often more compact cocoon, which is very cryptic against the bark of its host, tamarack (*Larix laricina*). The cocoon of *H. euryalus* tends to be ovoid to almost round, except for the valve end, somewhat resembling a Florence flask. The *H. euryalus*

cocoon is usually grey, and may be shiny in texture, but lacks the striations of *H. c. gloveri*. The larvae of *H. euryalus* usually spin the cocoon among the branches of the host plant. The cocoon of *kasloensis* is intermediate between *H. c. gloveri* and *H. euryalus* in shape and texture, possessing the banding of *H. c. gloveri*, but usually not as compact. I have collected only two cocoons of *kasloensis* in the wild; both were spun among dense vegetation, but not at ground level. In captivity larvae spun cocoons among leaves of the host, and, like reared *H. c. gloveri*, in the lower folds of the sleeve.

Comparative Life History.—All members of *Hyalophora* are univoltine, with adults emerging in the spring in temperate regions. Southern Arizona populations of *H. c. gloveri* often emerge during the late summer monsoon season, sometimes preceded by a facultative partial emergence during spring rather than a true bivoltine flight (Tuskes et al., 1996). The adult flight season is short, usually lasting three to four weeks. Adult males are strong fliers, as shown in various dispersal studies (Collins, 1984). In mark-and-recapture studies using virgin females as bait, male *H. cecropia* commonly flew over 5 km over several nights and one male was taken 12.5 km from the point of release. The dispersal potential of females is not well known, as no reliable method for tracking or recapture is available. Newly mated females are heavily laden with ova, but may fly greater distances as they finish oviposition. Potential rates of gene flow must be high in *Hyalophora*, an important parameter in the formation and maintenance of hybrid zones.

The larvae of all species feed on shrubs and trees and mature in about six to eight weeks. With the important exception of northern populations of *H. c. columbia*, most populations of all taxa tend to be polyphagous (Table 8). Perhaps the most polyphagous species is *H. cecropia*, although this tendency may be exaggerated by its ability to thrive in suburban situations where the larvae feed on ornamentally planted shrubs and trees, including exotics (Scarborough et al., 1974). Willows (Salicaceae), rosaceous shrubs and small trees, Ericaceae, and Rhamnaceae are common hosts shared by both *H. euryalus* and *H. c. gloveri*. These species differ in the acceptance of Douglas fir (*Pseudotsuga menziesii*) by *H. euryalus* and the use of Elaeagnaceae by *H. c. gloveri*. The northeastern populations of *H. c. columbia* appear to feed exclusively on larch or tamarack (*Larix*), a deciduous conifer, although populations in Manitoba and Ontario transitional to *H. c. gloveri* feed also on Betulaceae and various *Prunus* (Rosaceae) (Kohalmi and Moens, 1975, 1988).

The natural hosts of *kasloensis* are not well known. I collected two cocoons in the study area on western choke cherry (*Prunus demissa*), and reared stock (a minimum of three broods of 20–30 larvae each for each host plant) on this host and on *P. emarginata*, as well as on various *Ceanothus*, *Rhamnus rubra*, *Salix exigua* (a common willow host of *H. euryalus* and *H. c. gloveri*), and *Elaeagnus angustifolius*. Morewood (1991) reared British Columbia stock of *kasloensis* on *Ceanothus sanguineus*, *Rhamnus purshiana*, and *Pseudotsuga menziesii*. In addition, I have reared two broods from the same Okanagan Valley region on *Shepherdia argentea*. McGugan (1958) listed *Shepherdia canadensis* as a host for *H. euryalus*, and although he did not differentiate interior from coastal records, this shrub is confined largely to the drier interior where *kasloensis* occurs. Stock of *kasloensis* from Montana (four broods of 10–20 larvae each) refused to accept *Pseudotsuga*, and this trait may distinguish these populations from the *kasloensis* in British Columbia. Based on rearing experience and the distributions of potential hosts, it seems reasonable to include *Ceanothus*, *Rhamnus*, *Elaeagnus*, *Shep-*

Table 8.—*Host plants of Hyalophora.*

Species	Family of host plant					
	Rosaceae	Salicaceae	Rhamnaceae	Ericaceae	Elaeagnaceae	Pinaceae
<i>H. cecropia</i> ¹	<i>Prunus</i> <i>Malus</i>	<i>Salix</i>				<i>Acer</i>
<i>H. euryalus</i>	<i>Prunus</i> <i>Purshia</i> <i>Cercocarpus</i>	<i>Salix</i>	<i>Ceanothus</i> <i>Rhamnus</i>	<i>Arctostaphylos</i> <i>Arbutus</i>		<i>Betula</i> <i>Corylus</i>
<i>H. c. gloveri</i>	<i>Prunus</i> <i>Purshia</i> <i>Rosa</i> <i>Cercocarpus</i>	<i>Salix</i>	<i>Ceanothus</i>	<i>Arctostaphylos</i>	<i>Elaeagnus</i>	
<i>H. c. columbia</i> ²						<i>Larix</i>

¹ *Hyalophora cecropia* has been recorded from many other hosts (e.g., Scarbrough et al., 1974) including exotic, ornamental *Rhamnus*.

² Larvae of *H. c. columbia* near the blend zone with *H. c. gloveri* in Ontario and Manitoba also feed on *Prunus* and *Betulaceae*.

herdia, *Salix*, and possibly *Pseudotsuga* as natural hosts of *kasloensis*. Western larch (*Larix occidentalis*) is common in the Bitterroots in areas where *kasloensis* has been collected, including at high altitudes where other potential hosts are scarce, but I have been unable to confirm this probable host nor have I attempted to rear larvae on it.

The hosts of the hybrid populations in the Boise, Idaho, region are not known, but *Prunus emarginata* is especially common where moths have been collected, and various willows and *Ceanothus velutinus* may also be natural host plants.

Morphometrics of Hybrid Populations

The discriminant functions generated from wing characters produced an accurate classification of reference groups (Table 9). All specimens in the *H. euryalus* reference sample were identified correctly, and only 9.7% were placed in class 2 (between *H. euryalus* and F_1 hybrids) when reclassified using Mahalanobis distances. The reference group for *H. c. gloveri* was placed correctly in *H. c. gloveri*, with the exception of one individual identified as an F_1 hybrid in the standard three-way classification. This specimen and two others were placed in class 4 based on distance values; two of the three were unusually small, and two of the three had some red scaling in the postmedial color band. Both of these traits occur occasionally in indisputably pure *H. c. gloveri* populations, but their coincidence in these specimens caused the misclassification. Predictably, the laboratory F_1 hybrids showed the most variability, although 93.4% were correctly identified in the standard classification, and 91.2% were in class 3 (F_1 hybrids) in the five-class scheme based on distance values. Accuracy of the classification of wild specimens was confirmed by the three nearly nonoverlapping clusters of scores for reference samples plotted on the first and second canonical variables (Fig. 2).

There is an obvious trend in phenotypic variability from essentially pure *H. c. gloveri* at the Continental Divide near Helena, Montana, and the Pony, Montana, population to nearly pure *H. euryalus* on the western slopes of Lookout Pass, Idaho. Intervening samples show a smooth intergradation, with the highest frequency of F_1 hybrid-like phenotypes near Missoula, Montana; 67.9% were classified as such in the standard classification, and 53.6% were placed in class 3 based on distances (Fig. 3). Individual specimens were placed in all classes except for class 5, pure *H. c. gloveri*. Among the samples, *H. euryalus*-like individuals are found near Missoula, Montana, and *H. c. gloveri*-like moths are found west of the Continental Divide (Fig. 5).

Another zone of intergrades was found northeast of Boise, Idaho, in the drainage system formed by Mores Creek Canyon and Clear Creek Canyon from Idaho City to Banner Summit (Table 9; Fig. 4, 5). This sample of 55 moths contained individuals in all phenotypic classes in both classification schemes, although 76.3% were classed as F_1 hybrids in the standard scheme, and 69.1% were placed in the corresponding class 3 based on distance scores. These moths have a larger forewing length on average than those from Missoula (56.6 vs. 54.0 mm), and many appear more brightly colored (Fig. 6). Pure *H. c. gloveri* is found approximately 40 km west of the Sun Valley/Ketchum area in the Sawtooth National Forest, but the few adults taken 30 km to the northwest in Atlanta appear to be intergrades.

A third area of intergradation was found in the vicinity of Lost Trails Pass, near the intersection of the Continental Divide and the Bitterroot range. Moths of

Table 9.—Classification (number of specimens, percentage) of *Hyalophora* populations based on discriminant analysis of wing characters, with *H. euryalus*, *H. columbia gloveri*, and their F_1 hybrids as reference groups. Phenotypic classes derived from Mahalanobis distance values.

Sample groups (number)	Three-way classification				Phenotypic class				
	<i>H. euryalus</i>	Hybrid	<i>H. c. gloveri</i>	<i>H. euryalus</i>	2	3	4	5	
1a. West Lookout Pass, Idaho (Sweadner specimens) (16)	12 75.0	4 25.0	0 0	9 56.3	4 25.0	3 18.2	0 0	0 0	
1b. West Lookout Pass, Idaho (40)	20 50.0	20 50.0	0 0	15 37.5	5 12.5	20 50.0	0 0	0 0	
2. East Lookout Pass, Montana (Sweadner specimens) (33)	20 60.6	13 39.4	0 0	14 42.5	8 24.2	11 33.3	0 0	0 0	
3. West Lolo Pass, Idaho (8)	3 37.5	5 62.5	0 0	1 12.5	4 50.0	2 25.0	1 12.5	0 0	
4. East Lolo Pass, Montana (30)	13 43.3	16 53.3	1 3.4	4 13.3	9 30.0	15 50.0	2 6.7	0 0	
5. Missoula, Montana (28)	8 28.6	19 67.9	1 3.5	4 14.3	4 14.3	15 53.6	5 17.8	0 0	
6. Bearmouth, Rock Creek, Montana (16)	1 6.2	5 31.3	10 62.5	0 0	1 6.2	5 31.3	0 0	10 62.5	
7. Continental Divide (20)	0 0	0 0	20 100.0	0 0	0 0	0 0	2 10.0	18 90.0	
8. Sula, Montana (11)	3 27.3	6 54.6	2 18.1	2 18.2	1 9.1	3 27.4	4 36.2	1 9.1	
9. Gibbonsville, Idaho (21)	0 0	1 4.8	20 95.2	0 0	0 0	1 4.7	2 9.6	18 85.7	
10. Pony, Montana (22)	0 0	0 0	22 100.0	0 0	0 0	0 0	0 0	22 100.0	

Table 9.—Continued.

Sample groups (number)	Three-way classification				Phenotypic class				
	<i>H. euryalus</i>	Hybrid	<i>H. c. gloveri</i>	<i>H. euryalus</i>	2	3	4	5	
11. Mores Creek Canyon/Clear Creek Canyon, Boise County, Idaho, hybrid zone (55)	3 5.5	42 76.3	10 18.2	3 5.5	2 3.6	38 69.1	6 10.9	6 10.9	
F ₁ = <i>H. kasloensis</i> female (Ravalli County, Montana) × <i>H. c. gloveri</i> male (Lemhi County, Idaho) (13)	0 0	10 83.3	2 16.7	0 0	0 0	3 25.0	8 66.7	1 8.3	
F ₁ = <i>H. euryalus</i> female (Nevada County, California) × <i>H. kasloensis</i> male (Missoula County, Montana) (13)	11 84.6	2 15.4	0 0	4 30.8	7 53.8	2 15.4	0 0	0 0	
F ₁ = <i>H. c. columbia</i> female (Ontario, Canada) × <i>H. kasloensis</i> male (Ravalli County, Montana) (6)	0 0	2 33.3	4 66.7	0 0	0 0	2 33.3	2 33.3	2 33.3	
Reference <i>H. columbia gloveri</i> : Boulder, Colorado (33)	0 0	1 3.0	32 97.0	0 0	0 0	0 0	3 10.0	30 90.0	
Lab Reference F ₁ hybrids: <i>H. euryalus</i> × <i>H. c. gloveri</i> (45)	3 6.7	39 86.7	3 6.7	2 4.4	0	41 91.2	1 2.2	1 2.2	
Reference <i>H. euryalus</i> : northern California (31)	31 100.0	0 0	0 0	28 90.3	3 9.7	0 0	0 0	0 0	

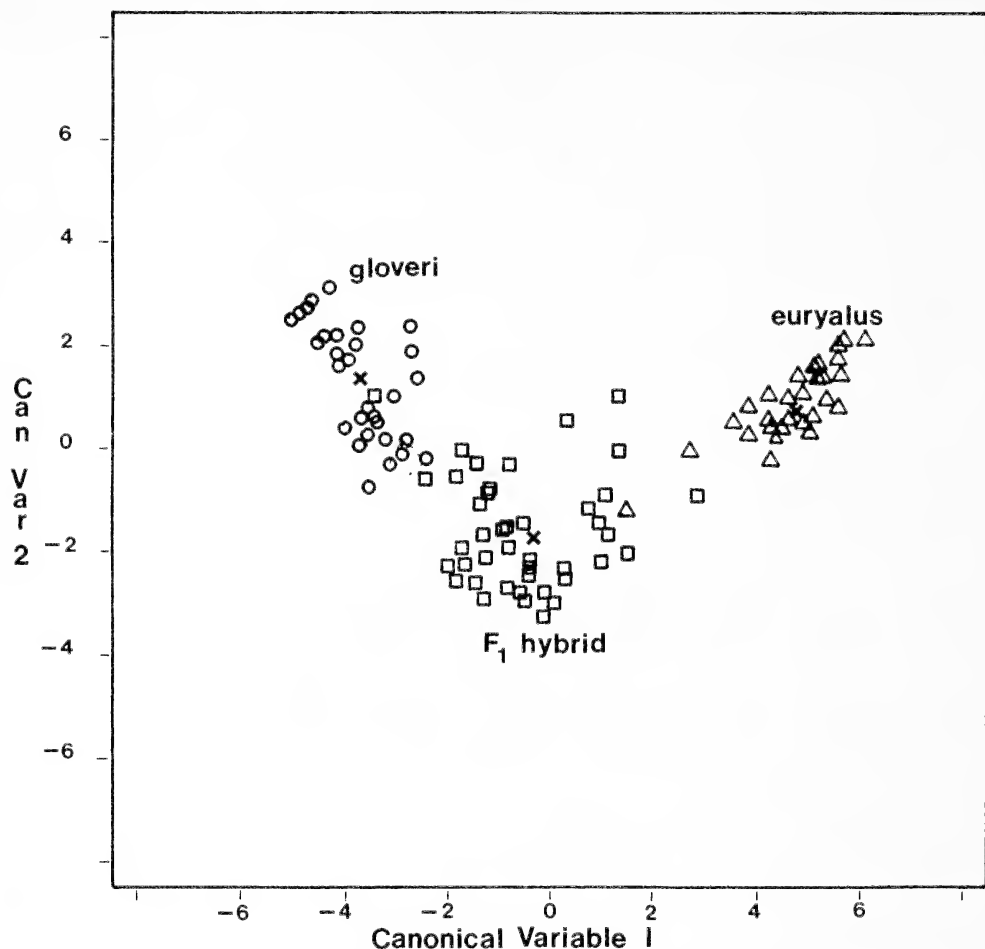


Fig. 2.—Scatter diagram of canonical variable scores from discriminant analysis of adult phenotypes from reference populations: *Hyalophora columbia gloveri*, *H. euryalus*, and their laboratory F_1 hybrids. X = group centroid.

the *kasloensis* phenotype (taken near Missoula) are found in Sula, just north of the pass, but nearly pure *H. c. gloveri* are found south over the pass near Gibbonsville, Idaho. However, three out of 21 males showed intermediate characters; one was placed in class 3 and two in class 4. The entire distribution of *Hyalophora* in western North America is shown in Figure 7.

DISCUSSION

Hybrid Origin of kasloensis and Other Intergrade Populations

Data gathered from morphometric analysis, examination of immature stages, experimental hybridization, and biogeography all support a hybrid origin of *Hyalophora* populations from the Bitterroot Mountains, referred to here as *kasloensis*. The geographic pattern of adult phenotypic variation corresponds to a hybrid zone and a majority of specimens were classified as hybrids using reared F_1

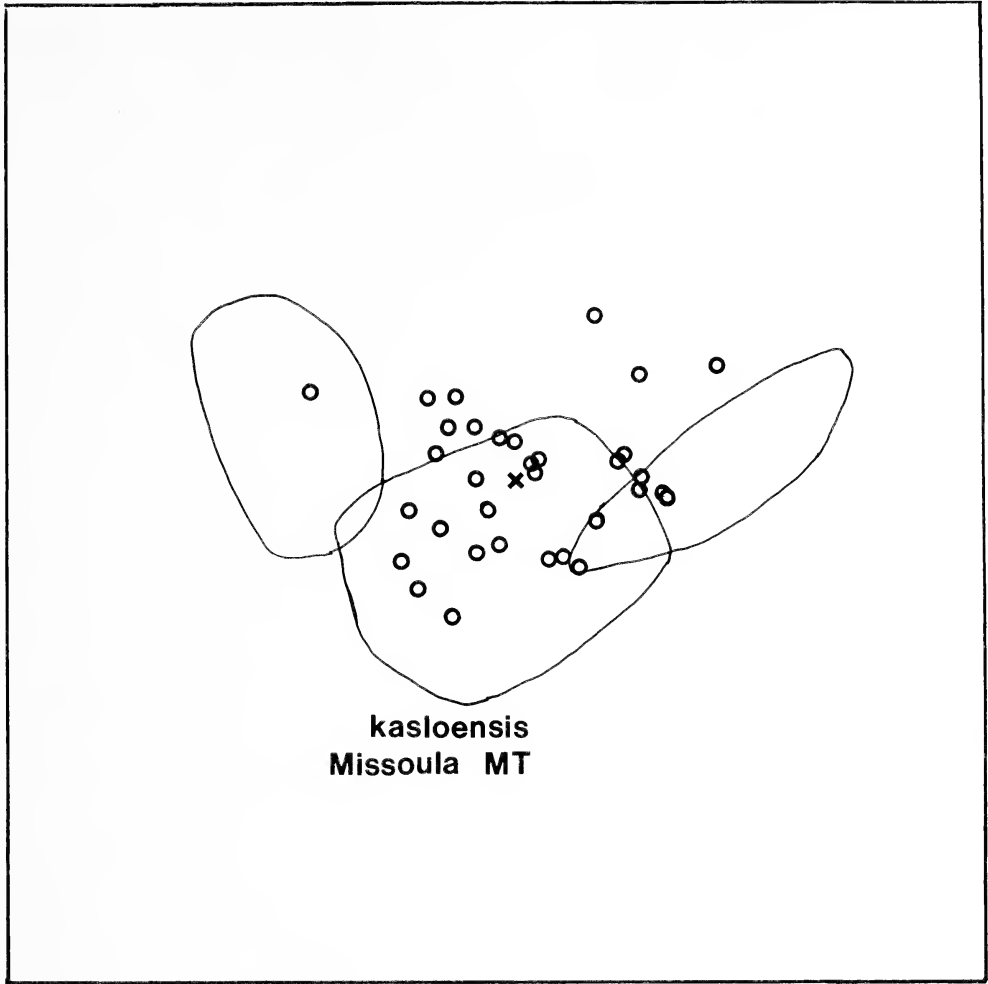


Fig. 3.—Scatter diagram of discriminant analysis scores of the Missoula, Montana, *Hyalophora* “*kasloensis*” sample population (Table 9). Distribution of reference sample scores shown in outline. X = group centroid.

hybrids as a reference series. Character clines exist that suggest hybridization and introgression, from *H. euryalus*-like phenotypes to the west to *H. c. gloveri*-like phenotypes in the east; this is especially apparent for the shape of the hindwing discal spot (Fig. 8). The first through fourth instars of *kasloensis* resemble *H. c. columbia* or *H. c. gloveri* more than corresponding instars of *H. euryalus*. The red to orange coloration of dorsal scoli in the final instar is unique to *kasloensis*, although the dorsal thoracic scoli of *H. c. columbia* are red. In fourth instars of *H. c. gloveri*, all dorsal scoli may be reddish, and perhaps in the mature *kasloensis* larva a disruption of gene regulation maintains the expression of this pigment into the next instar. A wide range of developmental incompatibilities are known in hybrids of Lepidoptera (Oliver, 1979, 1980) and of other organisms (Berven and Gill, 1983; Woodruff, 1989). Hybrid larvae reared from *H. euryalus* × *H. c.*

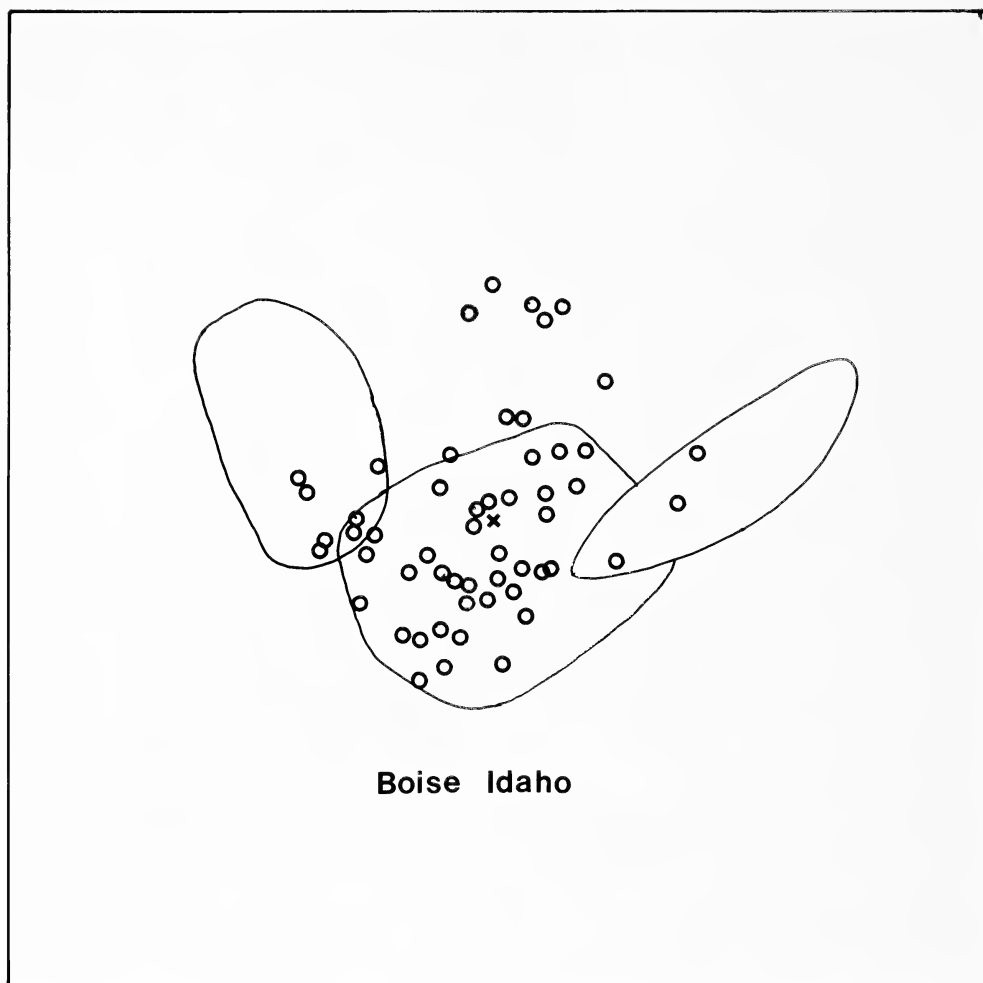


Fig. 4.—Scatter diagram of discriminant analysis scores of the Boise, Idaho, *Hyalophora* hybrid population. Distribution of reference sample scores shown in outline. X = group centroid.

gloveri crosses all had yellow dorsal scoli in the last instar; I have no data on larval coloration in *H. euryalus* \times *H. c. columbia* larvae. The cocoon of *kasloensis* is intermediate in shape and texture between *H. euryalus* and *H. c. gloveri*.

Significant reproductive incompatibility occurred in experimental crosses between *kasloensis* and both *H. euryalus* and the subspecies of *H. columbia*. This incompatibility was expressed in fertility, viability, and sex ratios of F_1 broods for at least one of the reciprocal crosses between *kasloensis* and the other taxa. The genetic compatibility in hybrids between *H. euryalus* and *H. c. gloveri*, including stock bordering the California Sierra Nevada hybrid zone, was much higher than for hybrid crosses between *kasloensis* and the two latter species. Hybrid unfitness in crosses between *H. euryalus* and *H. c. gloveri* is usually associated with F_1 hybrid female sterility, but ova hatch rates and adult sex ratios are normal (Collins, 1984). Compatibility between *kasloensis* and *H. euryalus*

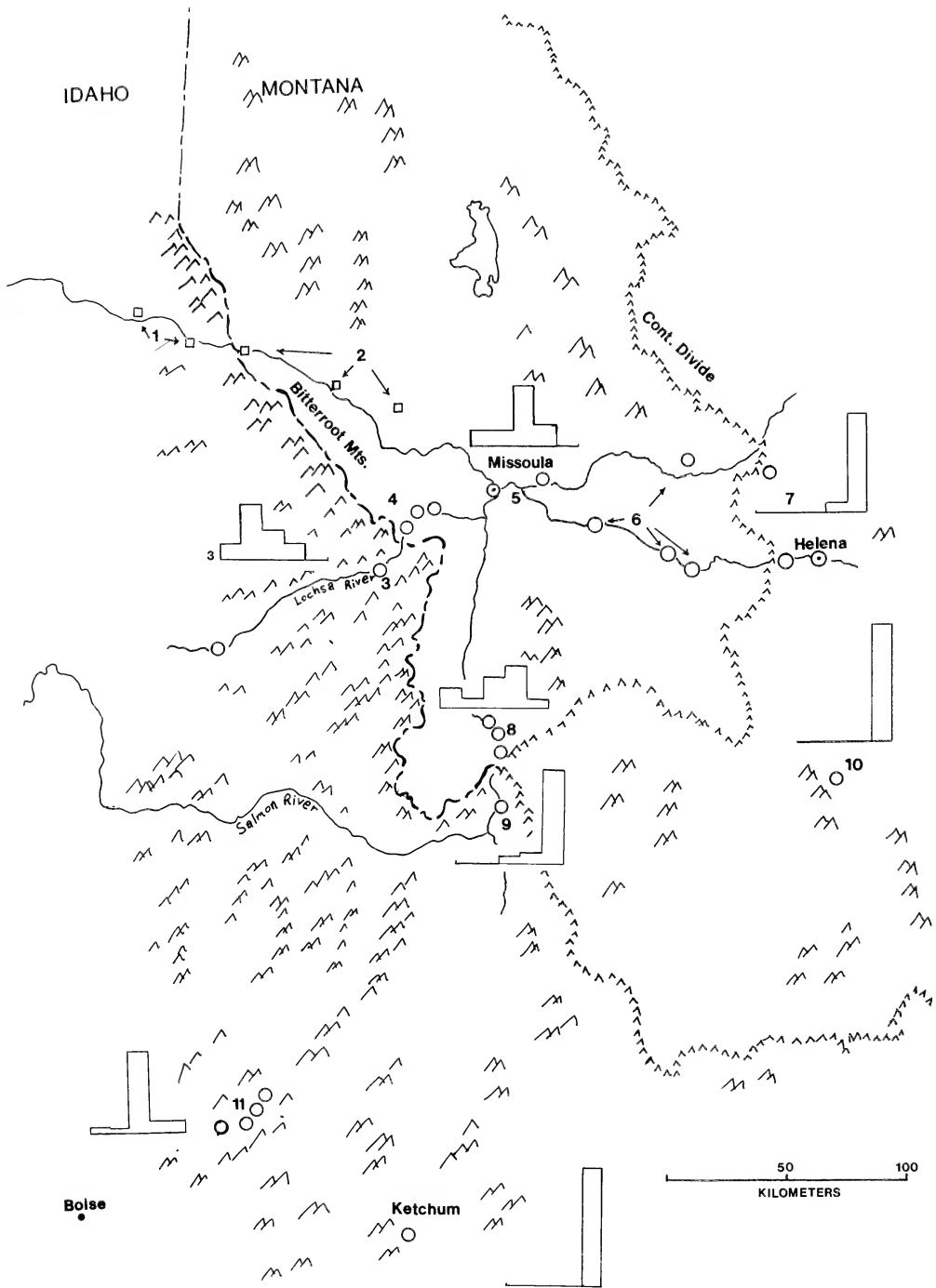


Fig. 5.—Geographic distribution of adult phenotypes for the Bitterroot Range *Hyalophora* hybrid zones. Phenograms based on discriminant analysis scores plotted as five classes from pure *H. euryalus* (left) to pure *H. c. gloveri* (right). Site numbers correspond to those listed in Table 9. Phenotypes collected near Ketchum, Idaho, appear to be pure *H. c. gloveri*; sample too small for analysis.

was variable, with certain crosses expressing a low fertility rate (Table 1: group III, crosses 2, 5) and others a low viability (Table 1: group IV, cross 1), but in general the compatibility with *H. euryalus* was higher than that seen in crosses between *kasloensis* and *H. c. gloveri* (Table 1: groups VII, VIII). Both fertility and viability were depressed in several such crosses involving female *H. c. gloveri*.

If genetic compatibility is taken as a measure of genetic similarity, then *kasloensis* would be seen as genetically distinct from *H. euryalus* and even further removed from *H. c. gloveri*, using experimental interpopulation crosses within these two species as a standard of comparison. Results of experimental hybridization do not support considering *kasloensis* to be a subspecies of *H. euryalus*, but instead point to a significant degree of developmental incompatibility in hybrid crosses between *kasloensis* and all other *Hyalophora*; a ranking by increasing incompatibility would be *H. euryalus*, *H. c. columbia*, and *H. c. gloveri*. In addition, a significant incompatibility was found in crosses between distant populations of *kasloensis*, indicating a degree of geographic genetic differentiation not found in other *Hyalophora*.

The clinal variation in the *kasloensis* adult phenotype revealed by morphometric analysis theoretically could result from either primary or secondary intergradation (Endler, 1977). The geographic location of the zone is consistent with a secondary contact resulting from a postglacial recolonization from refugia in the Sierra Nevada (*H. euryalus*) and from the Southwest and southern Rocky Mountains (*H. columbia*). Morphometric analysis of the Boise intergrade zone strongly suggests a hybrid origin for this population as well (Table 9). In a preliminary allozyme survey of the Sierra Nevada hybrid zone, Collins et al. (1993) found polymorphism in nine of 20 loci tested; the genetic identity index between *H. euryalus* and *H. c. gloveri* was 0.932. Clines across the hybrid zone in frequencies of nonfixed alleles corresponded to expectations based on gene flow. One locus was fixed for alternative alleles in *H. euryalus* vs. *H. c. gloveri*, with heterozygotes present only in the hybrid zone. A sample of six adults from the Boise population was also heterozygous for this locus, corroborating the proposed hybrid origin for this population. No comparative data were available on the allozyme composition of adjacent parental populations, and a comprehensive survey of all these Pacific Northwest populations is pending.

The presence of hybrid zones (indicating a degree of reciprocal gene flow in parapatry) and the genetic compatibility seen in experimental hybridization (Table 1) would support a closer relationship between *H. euryalus* and *H. c. gloveri* than between either of these species and *H. cecropia* (Table 7). Compared to crosses of *H. euryalus* \times *H. c. gloveri*, premating isolation and postzygotic barriers are more effective in hybrid crosses between *H. cecropia* and its congeners, and extensive hybridization does not occur in nature in areas of sympatry between *H. cecropia* and the subspecies of *H. columbia*.

Experimental Hybridization, Phylogenetic Inference, and Species Limits

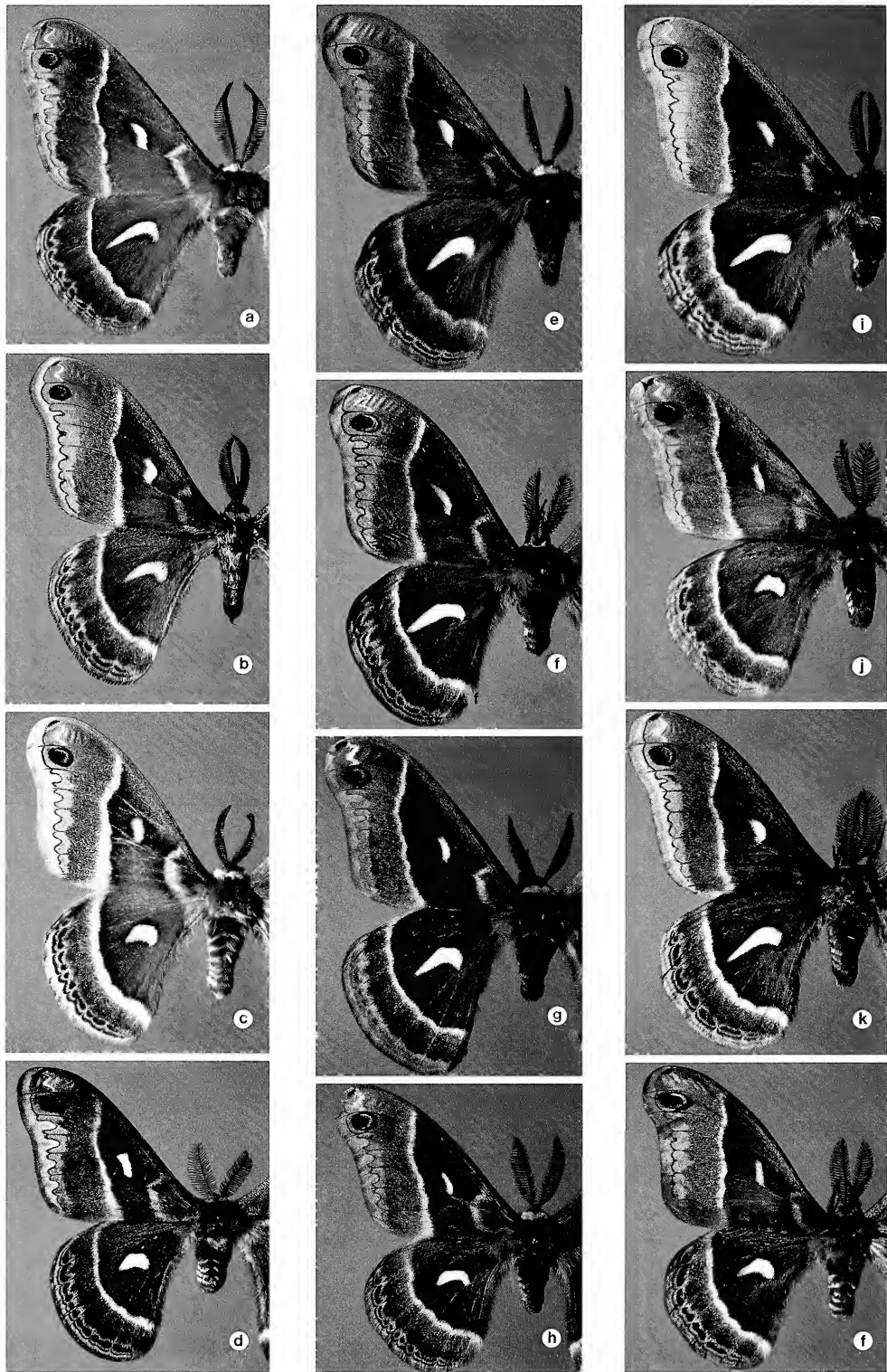
Experimental hybridization, as a means of measuring reproductive and developmental compatibility, traditionally has been employed to investigate taxonomic relationships, both at the species level and above (Remington, 1958). Even with the development of molecular techniques in genetic analysis, laboratory hybridization remains the most effective technique to reveal differences in genes controlling reproductive isolation among closely related species (Templeton, 1981).

Recently, however, reproductive compatibility has been considered to be a shared, ancestral trait among closely related taxa and therefore inappropriate for use in phylogenetic inferences (Cracraft, 1983, 1989; Zink, 1988; Frost and Hillis, 1990). Moreover, practical difficulties arise in entering hybrid character data into cladistic analysis due to the intrinsically reticulate nature of hybrid phenotypes (Wagner, 1983; McDade, 1992). Degree of postzygotic isolation may not indicate species relationships reliably. Hillis (1988) recognized several new species of leopard frogs (*Rana*) on the basis of mating-call differences in sympatric populations, morphology, and allozyme studies. The majority of interspecific crosses produced offspring capable of metamorphosis, but in virtually all cases the hybrid progeny showed some reduction in fitness. This reduction in fitness was not well correlated with phylogenetic relationship inferred from allozyme analysis. Morphological evolution is conservative among the leopard frogs, and hybrid compatibility often showed a correlation with adaptation to similar ecological conditions during development, even in crosses between species judged otherwise to be distantly related.

An opposing point of view holds that postzygotic barriers may arise incidental to genetic changes during speciation, and that such traits are useful in systematics because they reflect the history of genetic divergence of the taxa in question, and directly affect the potential of previously allopatric populations to maintain genetic integrity upon secondary contact (Templeton, 1989; Avise and Ball, 1990; Highton, 1990, 1995). These authors cite the extensive data on the genetics of species differences in *Drosophila*, as discussed by Orr (1987) and Coyne and Orr (1989a, 1989b). Male hybrid sterility typically is produced by incompatibility in gene action between loci on the X chromosome and autosomes, and female sterility is due largely to disruption of X chromosome–cytoplasm interaction. With increasing phylogenetic distance between the *Drosophila* parent species, the fitness of their hybrid progeny gradually decreases. A similar correlation between genetic incompatibility and phylogenetic distance, although less well documented, appears to be true for Lepidoptera (Oliver, 1979, 1980; Lorković, 1985; Collins, 1991; Ae, 1995).

By the “recognition species concept” (Paterson, 1985), the entire *Hyalophora* assemblage could be considered a single species, although this viewpoint would ignore obvious phenotypic, genetic, and ecological differentiation. Avise and Ball (1990) described a species concept incorporating aspects of both the phylogenetic concept (Cracraft, 1983) and species concepts based on genetic cohesion among component populations of a species (e.g., Templeton, 1989; Mallet, 1995). Avise and Ball (1990) review methods for determining “genealogical concordance” by inferring phylogeny from geographical patterns of gene sequences (e.g., mtDNA). Like the phylogenetic species concept, this approach seeks to determine ancestor–descendant lineages, but it also recognizes the importance of reproductive isolation to genetic and phylogenetic divergence.

Hyalophora in many ways are especially suitable for experimental measurement of genetic cohesion with respect to species limits. Data on genetic compatibility, available from laboratory pairings and analysis of natural hybrid zones, can provide an estimate of genetic cohesion within groups defined by other measures, such as geographic patterns in morphological or molecular characters. Hybrid zones are evidence of significant phylogenetic divergence between taxa and are maintained by barriers to gene flow due to hybrid incompatibility at critical loci. In *Hyalophora* the underlying fitness loci appear to regulate oögenesis. Careful



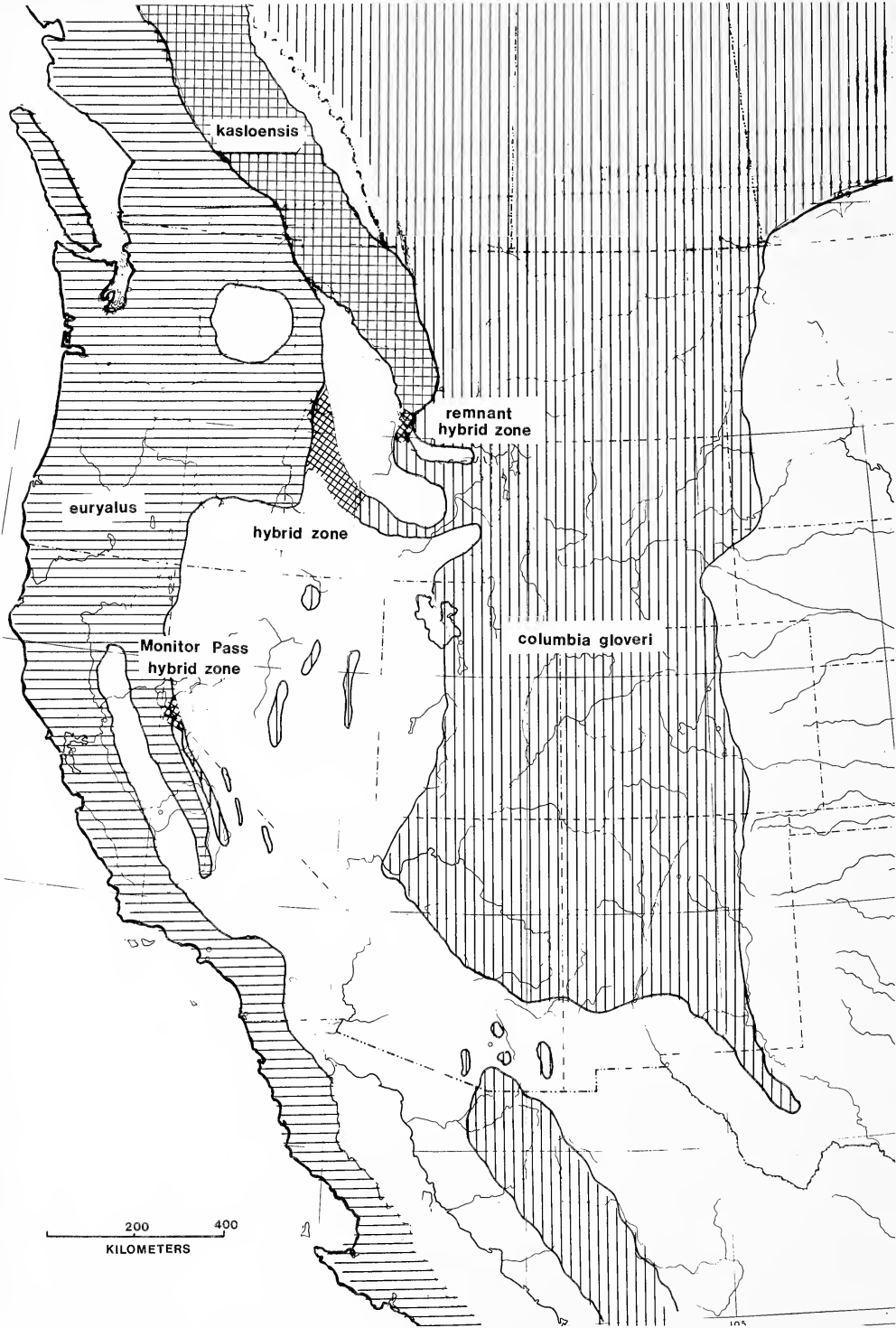
genetic analysis of hybrid zones can potentially reveal the basis of discontinuities in genetic cohesion among closely related taxa (Mallet and Barton, 1989a, 1989b; Sperling and Spence, 1990; Sperling, 1993a; Hagen and Scriber, 1995), which can be compared with phylogenetic hypotheses derived from independent data sets. Correlations between genetic discontinuity and phylogenetic relationships may reveal the pattern of divergence during speciation for genes regulating postzygotic compatibility.

Sterility in hybrids, skewed sex ratios, and other abnormalities confined to one sex are all examples of "Haldane's rule," the predominant expression of hybrid unfitness in the heterogametic sex. In a model proposed by Coyne and Orr (1989a), recessive alleles that are beneficial accumulate through mutation at loci on the sex chromosomes. In the heterogametic sex (females in Lepidoptera), these alleles pleiotropically interact with autosomal genes to regulate the expression of sex-related traits such as those associated with reproduction. Gene expression in hybrids of the heterogametic sex is disrupted, producing inviability, sterility, or other abnormalities. This model both explains the basis of single-sex hybrid unfitness and provides testable hypotheses of genetic divergence during speciation. In a companion study of speciation patterns in *Drosophila*, Coyne and Orr (1989b) concluded that newly diverged taxa produce sterile or subvital male hybrids (the heterogametic sex), but that female sterility evolves at a slower rate. Hagen and Scriber (1995) interpreted their extensive study of speciation in the tiger swallowtail butterflies (*Papilio*) in terms of these models and found an overall agreement with predictions for inheritance patterns of diapause problems and distorted sex ratios in hybrids; sex-linked species differences may be common in Lepidoptera (Sperling, 1994). Orr (1995) presented a mathematical model of speciation based on homologous loci in diverging taxa in which derived alleles produce incompatibility in hybrid genomes. This model predicts an increase in probability of speciation (postzygotic isolation) at a rate much faster than linearly with time. These results also predict that postzygotic isolation may arise sooner than either prezygotic isolation or divergence in traditional morphologic taxonomic characters.

Female sterility in interspecific *Hyalophora* hybrids is widespread, but hybrids are viable and developmental incompatibility typically is not severe. Interspecific female hybrids among the closely related *Callosamia* also are sterile, and inviability and developmental abnormalities are more severe than within *Hyalophora* (Haskins and Haskins, 1958; Peigler, 1977). Female sterility is the rule in other saturniid hybrids (Tuskes et al., 1996), even in hybrids between the semispecies

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Fig. 6.—Variation in *Hyalophora* adult phenotypes. a, *Hyalophora euryalus*. California, Siskiyou County, 3 mi E McCloud, 3 July 1971. b, F₁ hybrid = *H. euryalus* ♀ California, Ventura County, Mulholland Canyon × *H. columbia gloveri* ♂ Nevada, Elko County, Ruby Mountains, ecl. 16 May 1992. c, *Hyalophora columbia gloveri*. Montana, Madison County, S Pony, Tobacco Root Mountains, 15 June 1983. d, *Hyalophora c. columbia*. CANADA, Manitoba, 13 mi W Braintree, 15 June 1966. e–h, *Hyalophora* "kasloensis." e, Idaho, Idaho County, Wildgoose Campground, 20 mi E Kooskia, 9 June 1989; f, Montana, Missoula County, Bearmouth, 9 June 1989; g, Montana, Missoula County, 3 mi E Milltown, 10 June 1989; h, Montana, Missoula County, Rock Creek, 8 June 1989. i–l, *Hyalophora* hybrid intergrades. i, Idaho, Boise County, 25 mi N Idaho City, 10 June 1993; j, Idaho, Boise County, 12 mi N Idaho City, 10 June 1993; k, Idaho, Boise County, 14 mi N Idaho City, 10 June 1993; l, Idaho, Boise County, 25 mi N Idaho City, 10 June 1993. All specimens males, × .60; to caged females (except b).



Saturnia mendocino and *S. walterorum* (Tuskes and Collins, 1981). By circumventing natural mating barriers, breeders of saturniids have produced various intergeneric hybrids that show predictably increased developmental incompatibility (Peigler, 1978; Carr, 1984; Weast, 1989; Tuskes et al., 1996). In spite of losses due to hybrid unfitness, the successful production of any such intergeneric hybrids is evidence that the genes controlling basic morphogenesis are fundamentally similar in these genera, and therefore are evolutionarily conservative. In hybrids between the North American *Callosamia* and Asian *Samia*, phenotypes of larvae, cocoons, and adults are not distorted or disrupted, but often are strikingly intermediate in comparison to the differences between the parental species. By contrast, hybrid female sterility appears to be the most widespread manifestation of genetic incompatibility in interspecific hybrids in the Saturniidae and in other Lepidoptera families. This pattern suggests that developmental incompatibility, especially for genes controlling oögenesis, derives either from genetic differentiation during the speciation process or shortly thereafter. Progressively more severe disruption of development is seen as phylogenetically more distant taxa are crossed.

Pleistocene Environments and the Origin of Hyalophora Hybrid Zones

Climatic changes during the Pleistocene obviously had a profound effect on the distribution and abundance of organisms, and consequently also influenced genetic differentiation and speciation (Vrba, 1985; Hewitt, 1993). Lepidoptera leave very few fossils, with none known from the Quaternary, so that biogeographic and phylogenetic inferences must be made from living forms and from the fossil remains of their modern host plants (e.g., Tuskes and Collins, 1981). Even assuming that present-day host plants reflect ancient associations, inferring historical range changes in the *Hyalophora* from fossil plant remains is made more difficult by the polyphagy of the various species. Consequently, in the following discussion I assume a degree of polyphagy for the progenitors of modern *Hyalophora* taxa. All recognized species are to varying degrees ecological generalists, and throughout their ranges occupy a wide variety of climates and plant communities.

During the Cenozoic Era a warm, moist climate prevailed in North America and, until the Rocky Mountains formed late in the era, a tropical flora occupied a vast area with little east-to-west differentiation (Daubenmire, 1975; Mathews, 1979). Miocene fossils in northern Idaho and eastern Washington show remnants of a mixed forest of temperate deciduous trees combined with a few evergreen angiosperms, such as *Arbutus*. During this time many tree species disappeared, including *Juglans*, *Liquidambar*, *Sassafras*, and *Magnolia*. The Madro-Tertiary flora evolved as xeric-tolerant sclerophylls, probably first appearing in the lee of the mountain ranges then forming (Axelrod, 1977). During the Miocene this flora occupied much of California and central Nevada. The Madro-Tertiary flora was displaced toward the West Coast as the climate became cooler and drier, producing the oak-madrone woodland and chaparral communities now widespread in Cali-

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Fig. 7.—Geographic distribution of *Hyalophora* in western North America. Based on the author's collecting records, published records (Peigler and Opler, 1993; Tuskes et al., 1996), and on estimations derived from host plant associations.

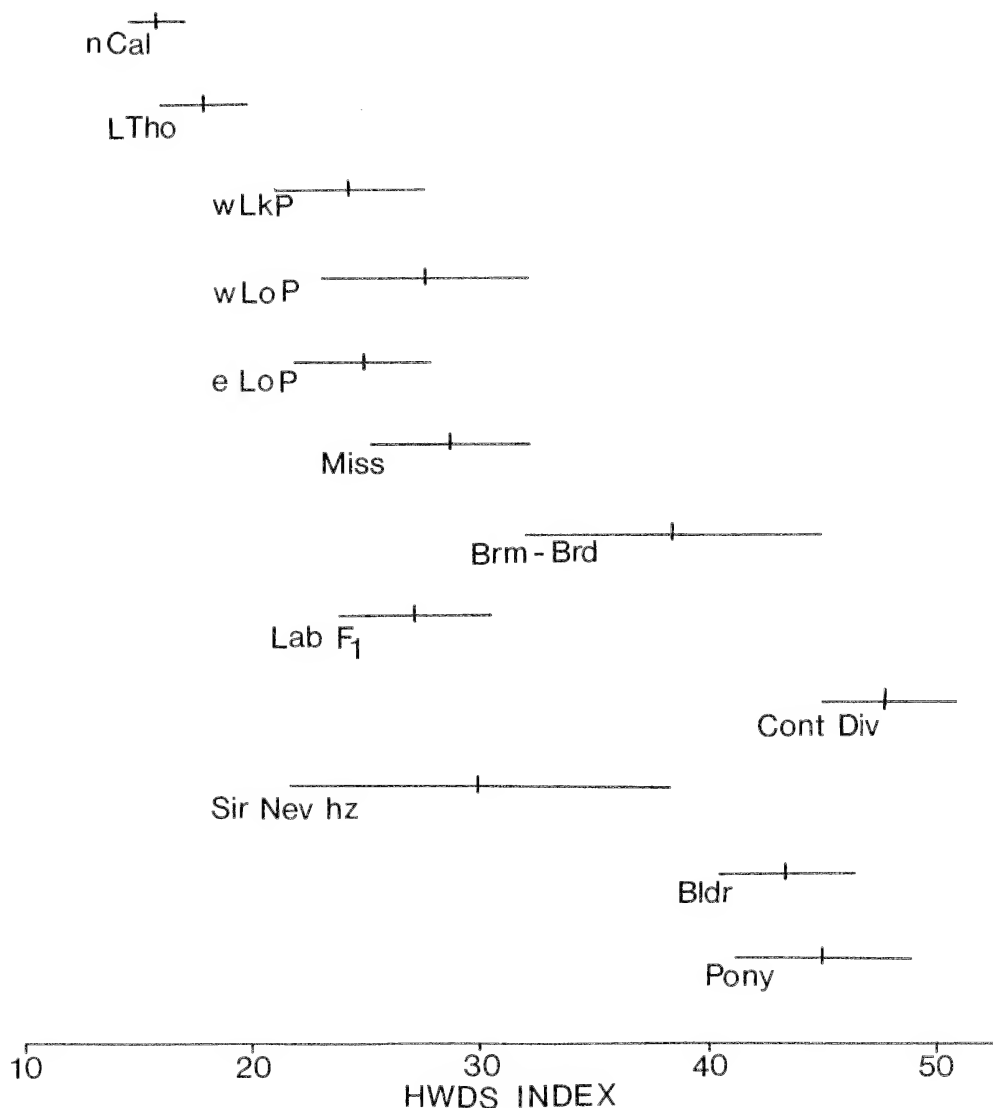


Fig. 8.—Phenotypic structure of the *Hyalophora* “*kasloensis*” hybrid zone and reference populations as shown by variation in the hindwing discal spot shape; mean and SD. Pure *H. euryalus*: northern California (nCal), Lake Tahoe (LTho); *H. kasloensis*: west Lookout Pass (wLkP), west Lolo Pass (wLoP), east Lolo Pass (eLoP), Missoula (Miss), Bearmouth to Brandon (Brm-Brd); laboratory F₁ hybrids (Lab F₁); pure *H. columbia gloveri*: Continental Divide (Cont Div), Sierra Nevada hybrid zone (Sir Nev hz), Boulder, Colorado (Bldr), Pony, Montana (Pony); Monitor Pass. Localities as listed in Table 9 and see Figure 5 for distribution of adult phenograms.

fornia. Another remnant of this once widespread flora is the evergreen oak woodland (associated with manzanita and madrone) now found in Arizona and the Sierra Madre of Mexico.

The family Saturniidae probably arose in the tropics of the New World, the region where the greatest saturniid diversity is found and where the more primitive

saturniid genera and families most closely allied with the saturniids occur (Michener, 1952; Lemaire, 1978; Tuskes et al., 1996). The saturniids apparently emigrated to the Old World, diversified, and reinvaded the New World, probably across the Bering land bridge connecting Asia with North America (Ferguson, 1971). The genera *Saturnia*, *Actias*, and *Antheraea* are diverse in the Old World, but each are represented by only a few species in the New World. The genus *Hyalophora* is found only in North America.

Many Lepidoptera fossils in the Oligocene Florissant shales appear to belong to modern genera (Emmel et al., 1992), and the antiquity of modern genera or even species may be generally true for other insect orders (Elias, 1994). Given the apparently conservative rate of evolution in the Lepidoptera, it seems reasonable to assume that the genus *Hyalophora* probably arose in the Cenozoic in North America. At the beginning of the Pleistocene, the *Hyalophora* may have consisted of three elements: the respective ancestors of *H. cecropia*, *H. columbia*, and *H. euryalus*. *Hyalophora cecropia*, or its immediate ancestor, probably evolved in the eastern deciduous woodland in association with many plant families in this center of plant diversity. The common ancestor of *H. columbia* and *H. euryalus* must have evolved in association with the Madro-Tertiary geoflora, with their larvae feeding on sclerophylls such as *Ceanothus*, *Rhamnus*, and *Arctostaphylos*. As the Rocky Mountains arose, the moths expanded their host range to include willow and various *Prunus* species. As the climate changed late in the Tertiary the *Hyalophora* became divided into a West Coast element (giving rise to *H. euryalus*) and a Rocky Mountain and Great Basin element (the ancestor of *H. columbia gloveri*).

The following summary of the last North American interglacial period (Sangamon), the final stage of glaciation (Wisconsin), and the postglacial Holocene is based largely on reviews by Wright and Frey (1965), Butzer (1971), Mathews (1979), Thompson (1988), and Pielou (1991). The climate during the Sangamon interglacial (ca. 80,000–70,000 YBP) is thought to have been somewhat warmer and wetter than at present, with a northward shift in the ranges of many tree species, and the distribution of *Hyalophora* in the Great Basin was probably more extensive.

The continuity of Cordilleran glacier complex in the west with the Laurentide ice sheet to the east is uncertain (Fig. 9), but the former was not directly connected to the glaciers present in the Cascade/Sierra Nevada ranges or with those in the Rocky Mountains. A cold, dry, windswept, treeless grassland steppe evidently occupied the lower elevations in the Great Basin, Rocky Mountains, and western Great Plains and much of the Great Plains and the Mississippi Valley was covered with windblown soil and sand. The Pleistocene and early Holocene flora of the Great Basin and desert Southwest has been reconstructed in great detail from examination of fossil pack rat middens (Van Devender, 1977; Van Devender and Spaulding, 1979), supplementing earlier work with fossil pollen records (Martin, 1963; Martin and Mehrlinger, 1965). During the Pleistocene the Great Basin was not invaded by alien tree species from either the Cascades or the Rockies, but rather the upper altitude limits of various plant zones shifted to lower elevations. A pine parkland was found in much of the Southwest, with pinyon-juniper woodland at comparatively lower elevations in much of the southern Great Basin, and the Mojave and Sonoran deserts. True desert probably was confined to the region of the Colorado River in southern California and adjacent Arizona, separated from the pinyon-juniper woodland by a band of sagebrush scrub and chaparral. Pine

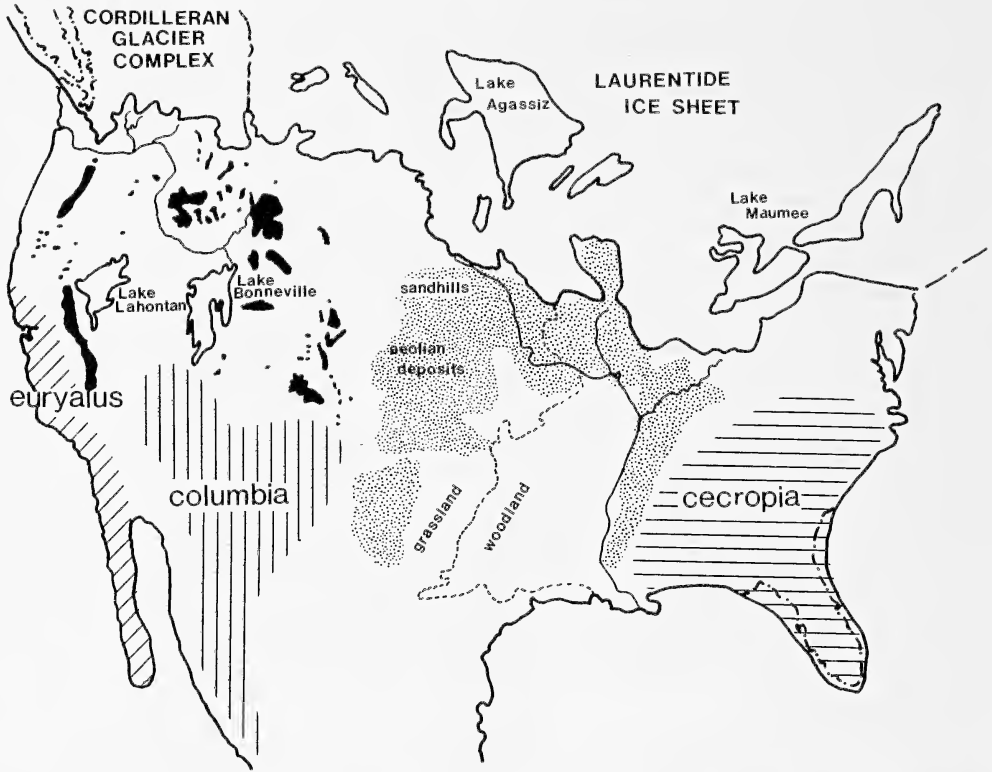


Fig. 9.—Hypothetical Pleistocene distribution of *Hyalophora* in North America during the Wisconsin stage of maximum glaciation. Geographic features based largely on Butzer (1971:fig. 57). Moth distribution based on paleobotanical and paleoclimatological data as cited in text.

forests mixed with scattered deciduous trees occupied the Southeast (Watts, 1980), grading into a spruce forest to the north. The West Coast south of the glaciers supported pine forests, with extensive glaciers forming in the High Sierra.

During the Wisconsin glacial maximum, *Hyalophora* probably would have been excluded from all but the southern extent of the present distribution. Populations of *H. euryalus* probably had an extensive distribution at low elevations in California and extending into Baja California. *Hyalophora c. gloveri* must have been restricted to the pinyon-juniper woodland of the Southwest and the southern Rocky Mountain region and isolated from *H. cecropia* by extensive dry grasslands and sandy regions to the east.

The recolonization of glaciated North America did not occur as a sequential northward movement of modern plant communities (Pielou, 1991). The rate of advance of each species depended on many factors including rates of seed dispersal, physiological tolerance, competitive interaction with other species, and distance from refugia. Some of the floral communities formed during postglacial times have no modern counterpart. Generally conifers invaded first, followed by a northward advance of deciduous hardwoods. As early as 14,000 YBP, shrubs colonized the grassland steppe bordering the retreating glaciers, and included the *Hyalophora* host plants silverberry (*Elaeagnus*) and buffalo berry (*Shepherdia*), and true willow (Lichti-Fedorovich, 1970). By 11,000–12,000 YBP, a spruce–

poplar–aspen forest had displaced this grassland, followed by birch, elm, ash, oak, and, lastly, pine. Many proglacial rivers and lakes were produced from melting ice, including those formed from buried ice; the latter are now the sites of prairie pot holes. A spruce–tamarack (*Larix*) muskeg formed in these mesic sites, much farther south than at present (Watts and Bright, 1968).

As the climate warmed these areas became warmer and drier and witnessed a sequence of changing forest flora: first balsam fir, then paper birch, white elm, burr oak, and finally (at about 8,000 YBP) the modern grassland of the Great Plains. To the east the retreating spruce forest was replaced sequentially by forests composed largely of jack pine, red pine, eastern white pine, firs, and finally by a mixture of paper birch, elm, and oak. In the west, lodgepole pine occupied a distribution corresponding to the eastern spruce forests, and was replaced by Douglas fir as the climate ameliorated (Axelrod and Ting, 1961; Axelrod, 1966; Baker, 1983).

The first *Hyalophora* colonizers east of the Rocky Mountains may have fed on the willows and Elaeagnaceae (*Elaeagnus*, *Shepherdia*). This association is now restricted to the Canadian Prairie Provinces, and it seems possible that the growing season may have been adequate to allow larval development at this early period preceding the plant succession that replaced the grassland steppe with forests. These *Hyalophora* populations subsequently may have adapted to feeding on *Larix* as the extensive spruce–tamarack bog/muskeg formed in the northern Great Plains. A brief period of warm climate, the Hypsithermal, occurred at about 8000 YBP, generally pushing plant communities northward and toward higher elevations in montane regions. The drying effect of the Hypsithermal was most severe in the rainshadow of the Rocky Mountains, where the modern prairie first developed and subsequently spread eastward. The present populations of larch-feeding *H. c. columbia* east of the Great Lakes probably represent a remnant of a much wider distribution, and may have been isolated from the larger subspecies *H. c. gloveri* by the spread of dry grasslands during the peak of the Hypsithermal.

Pioneer populations of *H. euryalus* probably exploited the northward movement of Douglas fir to colonize the coastal Northwest. Populations of *H. c. columbia* may have fed on western larch in the northern Rockies and hybridized with the conifer-adapted *H. euryalus* in the Bitterroot Range as both populations spread northward. *Hyalophora c. columbia* may have been displaced by *H. c. gloveri* from the south as hosts of the latter, such as *Prunus* and *Ceanothus*, became established in the northern Rockies. The present contact between the hybrid *kasloensis* populations and *H. c. gloveri* would then be secondary to the original hybridization event between *H. euryalus* and *H. c. columbia*. The rainshadow east of the Bitterroots must have been more severe during the Hypsithermal, perhaps isolating *kasloensis* from the *H. c. gloveri* east of the Continental Divide. Trapping data indicates that the density of *Hyalophora* and their hosts (except in riparian areas) decreases to the east of Missoula, which may explain the abrupt transition from the *kasloensis* phenotype to *H. c. gloveri* near the Continental Divide. The high Canadian Rockies appear to isolate *H. c. gloveri* from *kasloensis* to the west in the interior of British Columbia. During the Hypsithermal the grasslands of southeastern Washington and northeastern Oregon were probably more extensive and may have restricted gene exchange between *kasloensis* and *H. euryalus*. Antelope bitterbrush (*Purshia*) invaded the dry interior of British Columbia, Washington, and Oregon during this time (Daubenmire, 1969). Today this *Hyalophora* host is most common on the east slopes of the Cascades, but its historical distri-

bution probably was never extensive enough to provide a corridor between lower elevation populations of *H. euryalus* to the *kasloensis* in the Bitterroots.

The hybrid zone near Boise, Idaho, probably formed as *H. euryalus* invaded eastward from the Pacific Northwest toward present-day Coeur d'Alene, Idaho, then migrated southward along the western slopes of the Bitterroots. These populations would have been confined to a narrow band, bordered by the dry grasslands to the west, a restriction magnified by the Hypsithermal event. These *H. euryalus* populations would have met and hybridized with *H. c. gloveri* (then expanding north from the southern Rockies) but would have remained isolated from *kasloensis* by the high mountain ranges in southern Idaho.

A shift of plant communities to higher elevations during the Hypsithermal probably produced a period of hybridization between *kasloensis* and *H. c. gloveri* in the vicinity of Lost Trails Pass (between Sula, Montana, and Gibbonsville, Idaho). Today this summit does not support many potential hosts and is probably too high in the present climate to allow *Hyalophora* to breed. The small numbers of intergrades collected near Gibbonsville could represent a remnant of a past period of hybridization.

Hybrid Zone Models and the Status of kasloensis

A consensus of recent authors believes the majority of hybrid zones are "tension zones" where character clines are maintained by an equilibrium between selection and dispersal (Barton and Hewitt, 1985, 1989; Harrison, 1990; Hewitt, 1990). An alternative view holds that hybrid zones are maintained by heterozygote advantage in ecologically disturbed or marginal habitats (Moore, 1977). Advocates of the tension-zone model assert that the typical structure of hybrid zones—long, narrow bands of coincident character clines—are unlikely to be maintained by ecological superiority for so many seemingly unrelated loci. The *kasloensis* zone exhibits the hybrid unfitness typical of a tension zone, and the fact that all taxa of *Hyalophora* are ecological generalists further argues against the ecological superiority model.

The *kasloensis* zone would appear to be one of widest recorded hybrid zones (Barton and Hewitt, 1985:table 1). Width of the zone from Kooskia, Idaho, to near Helena, Montana, is nearly 300 km, about six times the width of the Sierra Nevada *Hyalophora* hybrid zone. Zone width is directly related to dispersal potential, and Barton and Hewitt (1985) ranked the Sierra Nevada zone among recorded maxima for both parameters, and exceeded only by those of two avian hybrid zones. Regional topography, ecological features, and historical factors also determine zone structure. Density of *Hyalophora* decreases west to east, probably in response to the rainshadow effect of the Bitterroots, and consequently gene exchange with *H. c. gloveri* at present may be restricted. To the north, the Canadian Rockies effectively isolate the two populations. Such a reduction of gene flow from one side would likely have the effect of broadening the zone; this effect is indicated in the broad, gradual intergradation into the *H. euryalus* phenotype to the west and the more abrupt transition into the *H. c. gloveri* phenotype to the east.

The reduced reproductive fitness in interpopulation crosses within *kasloensis* suggests strong genetic differentiation among the source populations used in these experimental crosses. Interpopulation incompatibility is not known for either *H. euryalus* or in *H. c. gloveri* (Collins, 1984). The origin of reproductive incom-

patibility within *kasloensis* relates directly to a model describing genetic differentiation of isolated populations within a species and subsequent hybridization upon range expansion (Barton and Hewitt, 1989; Hewitt, 1989, 1990, 1993). This process is most likely to occur during periods of severe environmental change when the species becomes geographically subdivided, as during the Pleistocene (Hewitt, 1993). In a heterogeneous environment, isolated demes are subject to differing selection regimes that, together with genetic drift, may produce unique, adaptive genotypes. At the end of the Pleistocene, isolated populations would expand their territory. Demes with the highest fitness would be the most successful colonizers, and would swamp out neighboring populations with less favorable gene combinations. Hybrid zones would form between these pioneer populations if heterozygotes suffered reduced fitness, and these zones might act as significant barriers to introgression (Hewitt, 1989). This barrier effect is magnified by the tendency of hybrid zones to migrate to areas of low population density (Barton and Hewitt, 1985). The formation of a mosaic of genetically distinct populations bounded by hybrid zones may determine a geographic pattern of speciation as each population undergoes further differentiation (Hewitt, 1993). Hybrid zones are evidence that allopatry is not essential for differentiation in the face of potential gene flow. Because the tension zone defines regions of local adaptive equilibria separated by adaptive valleys (the zone itself), they are comparable to Wright's (1932) shifting balance between selection on individuals within a population, and random drift and interpopulation selection (Barton and Hewitt, 1989).

A process of local fitness optimization or amelioration of incompatibility is also possible in hybrid zones. Selection might favor alleles that modify the detrimental effects of heterozygosity. Several authors have cited the disruption by recombination and gene flow from parental populations of any favorable gene combinations that might arise. This argument has been offered to explain the failure of reproductive isolation to evolve in hybrid zones (Bigelow, 1965; Barton and Hewitt, 1985; Butlin, 1989). However, Virdee and Hewitt (1994) found evidence for such a local amelioration within an orthopteran hybrid zone, and Collins (1984) hypothesized that this process had produced the fully fecund intergrade females that occur in the Sierra Nevada hybrid zone, in contrast to barren lab F_1 females when crosses were made between the parental populations bordering the zone. In these cases this process is comparatively localized and has not produced a fusion of the hybridizing populations. Such a process of amelioration seems to have occurred within the Boise hybrid zone, but to a lesser extent within *kasloensis*.

The process of isolation–differentiation–subdivision by hybrid zones might have occurred within the range of *kasloensis* in addition to the formation of the original hybrid zone upon secondary contact between *H. euryalus* and *H. columbia*. If the original contact was between *H. euryalus* and the small, dark, conifer-feeding subspecies *H. c. columbia*, this event could explain the dark coloration of adult *kasloensis*, the red coloration of the fifth instar scoli (due to hybrid disruption of the expression of red pigmentation in *H. c. columbia*), and the pattern of incompatibility seen in experimental crosses (greater isolation from *H. c. gloveri* than *H. c. columbia*). Populations currently recognized as *H. c. columbia* are probably descendants of frontier populations exploiting the colonization of deglaciated terrain by their host plant *Larix*. A subsequent hybrid zone between *kasloensis* and *H. c. gloveri* then would have been established as the latter moved northward, following the spread of their deciduous, shrubby hosts. Climatic os-

cillations during and after the Pleistocene may have disrupted these events by temporarily subdividing the distribution of *kasloensis* into smaller, isolated populations, some of which could have survived during glacial periods. The action of drift and selection, as outlined above, on such intrinsically genetically variable populations would increase the likelihood of differentiation. Given some degree of hybrid unfitness within newly isolated hybrid populations, selection within each to improve genetic compatibility would likely produce alternative genotypes, that in turn might be incompatible upon sympatry as a result of range expansion following glacial periods. What we now refer to as *kasloensis* might represent a mosaic of such populations, similar to the model envisioned by Hewitt (1989, 1993).

Obviously, these questions beg to be explored in more detail by means of molecular techniques. Mitochondrial DNA analysis would be especially useful in determining phylogenies among populations (Avise et al., 1992; Sperling, 1993b), and enzyme electrophoresis and DNA sequencing techniques could measure the extent of introgression across hybrid zones and possibly resolve the question of separate contributions by *H. c. columbia* and *H. c. gloveri* to a contact zone with *kasloensis*.

CONCLUSIONS

1. Morphometric analysis, immature phenotypes, experimental hybridization, and paleoclimate and paleoflora data all independently support the interpretation of a hybrid origin for *Hyalophora* "*kasloensis*" as a result of range expansion and secondary contact between *H. columbia* and *H. euryalus* following allopatric divergence during the Pleistocene. The *kasloensis* zone is very wide (300 km), possibly due to topography restricting gene exchange at present with *H. c. gloveri* to the east; more gradual intergradation with *H. euryalus* occurs to the west. Compared to other *Hyalophora* hybrid zones, experimental hybridization shows significant incompatibility between *kasloensis* and congeners in terms of fertility, embryo viability, hybrid sex ratios, and fecundity of hybrid females. In addition, interpopulation crosses within *kasloensis* show some degree of incompatibility in fertility, viability, and fecundity, but not in sex ratios of "pure" *kasloensis* broods. These findings suggest that *kasloensis* populations are genetically subdivided and conform to current models of genetic divergence and the formation of hybridizing populations in the context of Pleistocene and postglacial range changes. Molecular genetic studies are needed to determine the fine structure of the hybrid zones and to evaluate these models.

2. The hybrid zone near Boise, Idaho, is similar in geographic extent and phenotypic structure to the Sierra Nevada zone. Intergrade females are probably fully fertile, and males from this zone are genetically compatible in experimental crosses with females of *H. euryalus*, *H. c. gloveri*, and *kasloensis*. By contrast, females produced by *H. c. gloveri* \times *H. euryalus* crosses are barren when source populations are widely allopatric. A process of local optimization in compatibility appears to be operating within both the Boise and Sierra Nevada hybrid zones.

3. By traditional morphological criteria the *Hyalophora* have been divided into four taxa, a scheme not congruent with either prezygotic mating behavior or with postzygotic isolation. Some hybridization occurs where different recognized taxa are sympatric. All taxa apparently share a common pheromone and mate just before dawn, although slight differences in flight season and calling time partially

isolate *H. cecropia* from *H. c. columbia* (Tuttle, 1985). The well-defined hybrid zones between *H. c. gloveri* and *H. euryalus* contrast with the blend zone between *H. c. columbia* and *H. c. gloveri*, and experimental hybridization corroborates the division of *H. columbia* into two subspecies and recognition of *H. euryalus* as a distinct species. Hybrid-like specimens are produced only occasionally in contact zones between *H. cecropia* and congeners, and experimental hybridization also supports treating this taxon as a species distinct from *H. euryalus* and *H. columbia*. The formation and persistence of hybrid zones reveals significant discontinuities in genetic cohesion, and the taxa within *Hyalophora* conform to species concepts stressing this characteristic (Templeton, 1989; Avise and Ball, 1990; Mallet, 1995) but do not conform strictly to the biological species concept based on reproductive isolation. The origin of hybrid zones and taxonomic relationships within *Hyalophora* are consistent with paleoclimate reconstructions, but a test of phylogeny and species limits must await a cladistic analysis based on independent character sets.

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A PHYLOGENETIC CLASSIFICATION OF WATERFOWL
(AVES: ANSERIFORMES), INCLUDING SELECTED
FOSSIL SPECIES

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ABSTRACT

A summary classification of 175 modern species and 30 well-represented fossil forms of waterfowl (Aves: Anseriformes) is presented, based on a series of phylogenetic (cladistic) analyses of the group using morphological characters (Livezey, 1986a, 1986b, 1986c, 1989a, 1989b, 1990, 1991, 1993a, 1993b, 1995a, 1995b, 1995c, 1996a, 1996b, 1996c, 1997a, 1997b). The proposed classification includes a superordinal grouping with the Order Galliformes, and subdivides the Anseriformes into two suborders (Anhimae and Anseres), two superfamilies (Anseranatoidea and Anatoidea), and five families (Anhimidae, Anseranatidae, †Presbyornithidae, †Cnemiornithidae, and Anatidae). Among the latter, the Anatidae is the largest and comprises six subfamilies: Dendrocygninae (comprising two tribes and two genera), Dendrocheninae (two genera), Anserinae (four tribes, nine genera), Stictonettinae (one genus), Tadorninae (four tribes, 15 genera), and Anatinae (five tribes, 31 genera). The classification also incorporates: phylogenetic inferences and associated taxonomic decisions subsequent to the preliminary work by Livezey (1986a); corrections of classifications included with the earlier analyses; recognition of two species of comb-duck (*Sarkdiornis*); and provisional partitions of several problematic species groups (*Branta canadensis*, *Merganetta armata*, and *Somateria mollissima*). Also included are a concise historical review of the classification of the order, an assessment of the relative support documented for the taxonomic groups defined within the classification, and suggestions for future investigations.

INTRODUCTION

Brief History of Classification

Early Treatises.—The first comprehensive classification of waterfowl was that by Willughby and Ray (1676), in which known members of the Anseriformes were segregated from other aquatic birds (e.g., Sphenisciformes, some Rallidae, some Charadriiformes). This classification was a largely dichotomous scheme in which the Anseriformes were defined as swimming birds having webbed feet, short legs, and with toes arranged three forward and one (free) digit oriented backward; most members were defined further by the possession of a broad bill, the sole exception being the separately grouped, narrow-billed Smew (*Mergellus*) and mergansers (*Lophodytes*, *Mergus*). Within the larger group, Willughby and Ray (1676) partitioned members into the larger “goose-kind” (typified by the swans and true geese) and the smaller “duck-kind”; the latter group was subdivided further into the diving species or “sea-ducks” (typified by shelducks, eiders, scoters, goldeneyes, and scaup) and the “pond-ducks” (including the typical dabbling ducks).

The classification by Linnaeus (1758) was fundamental in the application of a binomial taxonomy. With respect to the waterfowl, however, Linnaeus (1758) adopted the primary segregation of mergansers proposed by Willughby and Ray (1676), although he placed the two groups adjacently within the eclectic “genus”

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Anseres together with a number of taxa currently assigned to other taxonomic orders. Linnaeus (1758) sorted the other 39 recognized taxa among groups characterized as having bills with "humped" bases (swans, shelducks, and scoters), bills having sides of the base equal (most anatids), variably recurved wings (miscellaneous domestic ducks), or crests (including American Wood Duck [*Aix sponsa*] and Tufted Duck [*Aythya fuligula*]).

Finding the scheme by Linnaeus (1758) impractical, Brisson (1760) proposed an alternative in which 26 orders of birds were distinguished on the basis of an enlarged suite of characters. The resultant classification was the first in which the typical waterfowl (here including the mergansers) were segregated from all other birds in a single higher taxon; the poorly known screamers were classified apart from other waterfowl, as they would be until the study by Parker (1863). Brisson (1760) divided the group into three subgroups, termed genera: "*Merganseris*" (mergansers), "*Anserinum*" (geese, swans, some sheldgeese, and the Common Eider [*Somateria mollissima*]), and "*Anatinum*" (other ducks).

The classification of waterfowl by Buffon (1784, 1786) represented, at best, stasis in the classificatory history of waterfowl. Moreover, Buffon (1784, 1786) obscured the foregoing advancements by segregating the mergansers from other ducks (placing them adjacent to the loons), and simply listing (essentially in order of decreasing size, without indicating explicit subgroupings) the species of waterfowl within a diverse series of avian taxa; most of the latter taxa corresponded to higher groups currently considered taxonomic families. The absence of an obvious classificatory structure in the works by Buffon prompted Pennant (1786) to prepare an index to the series that corresponded with his own, earlier classification (Pennant, 1781).

Latham (1785) closely followed the classification by Linnaeus (1758) with respect to the waterfowl; however, although he retained a separate "genus" for the mergansers, he placed them immediately before the "genus" for the ducks, geese, and swans. Bonnaterre (1791) included waterfowl among a number of other aquatic groups and some shorebirds in his fifth class of genera; the mergansers were listed before other ducks, geese, and swans, immediately following the skimmers (Charadriiformes: Rynchopidae). Illiger (1811) advanced the concept of the taxonomic family as a natural group of genera, and united the ducks, geese, and swans within the single family "Lamellosodontati," with the single exception of assigning the Cape Barren Goose (*Cereopsis novaehollandiae*) to the "Grallatores." A series of largely derivative works by Merrem (1813), Cuvier (1817), Vieillot (1818), and Temminck (1820) followed, most perpetuating the fundamental division between mergansers and other waterfowl first formalized by Wilughby and Ray (1676). Leach (1820) prepared the first classification of birds in which family names were based on type genera and were derived using the suffix "-idae," although whether the work meets all formal criteria of publication for purposes of seniority of family-group taxa remains a point of controversy (Bock, 1994; Olson, 1995).

Vigors (1825a) presented a quinarian arrangement of avian orders, the fifth of which comprised the waterfowl or Natatores. This division was partitioned further into five subgroups: (1) geese and swans, (2) *Cereopsis*, (3) dabbling ducks (*Querquedula* and other ducks lacking a lobed hallux), (4) mergansers, and (5) eiders and pochards. The singular placement of the poorly known *Cereopsis* as "transitional" between geese and ducks presumably stemmed in part from the earlier lapse by Illiger (1811). In a companion work, Vigors (1825b) provided a more

detailed classification of waterfowl, in which the waterfowl were restricted to the Family Anatidae of the Order Natatores, the latter also including four other families of water birds; the Anatidae were subdivided into the subfamilies Anserina (geese, including *Plectropterus*), Cereopsina (*Cereopsis*), Anatina (shelducks and dabbling ducks), and Cygnina (swans), as well as an unnamed subfamily for the seaducks (tentatively including *Mergus*), pochards, and stiff-tailed ducks.

Subsequent classifications of waterfowl based on quinarian or related perspectives include those by Yarrell (1827) and Swainson (1837). Classifications by Lesson (1828, 1831) were quinarian at least at ordinal and subordinal levels, within which he included waterfowl as a single family in an order including most aquatic birds (e.g., loons, grebes, penguins, alcids, and pelecaniforms). Lesson (1828) placed *Cereopsis* immediately following the typical geese, but later he (1831) listed the genus immediately before them. In both works, however, Lesson (1828, 1831) included *Mergus* as the last member of the ducks.

Eyton (1838) held strong biblical beliefs and considered higher classification to be a largely arbitrary exercise, but nonetheless prepared a classification of waterfowl based on anatomical characters (including osteological) comprising six subfamilies: Plectropterinae (including modern genera *Anseranas* and *Plectropterus*), Anserinae (*Cereopsis*, *Branta*, *Anser*, *Coscoroba*, *Cygnus*, *Sarkidiornis*, *Alopochen*, *Chloephaga*, *Tadorna* [part], and *Nettapus*), Anatinae (*Dendrocygna*, *Tadorna* [part], *Malacorhynchus*, *Cairina*, *Aix*, *Anas*, and *Marmaronetta*), Fuligulinae (*Tachyeres*, *Rhodonessa*, *Netta*, *Aythya*, *Polysticta*, *Somateria*, *Histrionicus*, *Camptorhynchus*, *Melanitta*, and *Bucephala*), Erismaturinae (*Thalassornis*, *Oxyura* [including *Nomonyx*], and *Biziura*), and Merginae (*Mergellus* and *Mergus* [including *Lophodytes*]). Eyton (1869) later produced an abridged version of this classification. Subsequent classificatory proposals by Gray (1841, 1871), Reichenbach (1849–1850), Bonaparte (1856), Baird et al. (1860), Sclater and Salvin (1876), Sclater (1880), Stejneger (1885), and Lydekker (1891), although not individually influential, contributed to the systematics of Anseriformes a number of minor taxonomic refinements and family-group names.

Fürbringer (1888) prepared a monumental summary of the comparative anatomy of birds, within which he delineated a number of taxonomic groups. In this scheme, the screamers were segregated from typical waterfowl, and within the latter the mergansers were considered distinct from other members. Although no classification of waterfowl was presented, the anatomical monograph by Parker (1890) contributed substantially to the osteological evidence for natural groups of Anseriformes. The syntheses by Gadow (1892, 1893) were important for the assessment of anatomical differences in a systematic context, but the included classifications of the waterfowl were rudimentary and accompanied by little explicit justification.

The most important systematic treatment of waterfowl to appear in the late 19th century was that by Salvadori (1895). Drawing largely from Sclater and Salvin (1876) and Sclater (1880), Salvadori (1895) arranged the waterfowl (Order Chenomorphae, here including the screamers and flamingos) in three couplets of suborders and families, the third (Anatidae) comprising 11 subfamilies. Salvadori (1895) formally grouped eight genera under the subfamilial taxon Plectropterinae, a group later to be modified for reference to the “perching ducks.” Salvadori (1895) also taxonomically distinguished the true geese (*Anser* and *Branta*) from the superficially similar sheldgeese (*Chloephaga* and *Cyanochen*) and Maned

Duck (*Chenonetta*), and grouped together three peculiar genera adapted to lotic habitats (*Hymenolaimus*, *Salvadorina*, and *Merganetta*).

Based on an anatomical study of the whistling ducks (*Dendrocygna*), Shufeldt (1914) altered the classification of the genus by Salvadori (1895) in elevating the genus to subfamilial rank. In his classic four-volume work, Phillips (1922, 1923, 1925, 1926) largely followed the subfamilial classification proposed by Shufeldt (1914), with most deviations from that scheme resulting from the deletion of "geese" (e.g., *Cyanochen*, *Chenonetta*) from this series dedicated to the "ducks." Among the important intuitions expressed by Phillips (1922) were the heterogeneity of the "perching ducks," the distinctness of the shelducks from the typical dabbling ducks, and intermediacy of *Heteronetta* between the surface-feeding and diving ducks.

In the first volume of the renowned "Check-list of Birds of the World," Peters (1931) classified waterfowl (including the screamers) in a single order comprising two couplets of suborders and families; the Anatidae were subdivided into ten subfamilies. The arrangement of genera among the latter resembled that by Salvadori (1895), but Peters (1931) made a number of changes, including the grouping of *Plectropterus* with *Anseranas*, the movement of some sheldgeese into the subfamily including the true geese, and the dismantling of the subfamily of "perching ducks." In a compilation of fossil birds, Lambrecht (1933) recognized ten subfamilies of the Anatidae; important deviations from contemporary arrangements included the essentially reversed sequence of subfamilies (Merginae first, Cygninae last) and inclusion of *Nettapus* with pochards in the Nyrocinae. Kuroda (1939) primarily followed the classification by Salvadori (1895).

Delacour, the Ethological Tradition, and Contemporary Works.—Inspired by the seminal ethological works of Heinroth (1911) and the ongoing behavioral analyses by Lorenz (1941), Delacour (1936, 1938) began a series of works on the systematics of Anseriformes primarily based on behavioral patterns. In a landmark work, Delacour and Mayr (1945) presented what was to become the most influential classification of waterfowl of the 20th century. The key innovation of the classification by Delacour and Mayr (1945) was the delineation of tribes within subfamilies; the resultant scheme (Table 1) divided waterfowl (screamers excluded) into two subfamilies, Anserinae (true geese, swans, and allies) and Anatinae (true ducks and allies). This classification was followed, with only minor changes, in a subsequent series of monographs (Delacour, 1954, 1956, 1959, 1964). Notable revisions in the latter series included the movement of *Anseranas* from the Cairinini to a monotypic subfamily; and the erection of the Tribe Somateriini for the eiders, after Humphrey (1958).

During this period, Boetticher (1929, 1936–1938, 1937, 1942, 1943, 1950, 1952) presented a number of intuitive evolutionary trees for selected subgroups of waterfowl based on anatomical and behavioral similarities, and proposed a series of increasingly detailed and hierarchically complex classifications. In a final synthesis, Boetticher (1952) presented a classification of waterfowl (excluding screamers) comprising two families, Anseranatidae (*Anseranas*) and Anatidae (other taxa). The Anatidae was divided into two subfamilies, Anserinae (subdivided into two tribes comprising four "sections" and five genera) and Anatinae (subdivided into seven tribes comprising 16 "sections" and 36 genera); in addition, subgenera were given parenthetically and selected groups of species encompassing several subgenera were indicated by brackets.

As part of a remarkably long series of works in which a number of innovative

Table 1.—Classification of modern genera of Anatidae (Anseriformes exclusive of Anhimidae) proposed by Delacour and Mayr (1945). Genera are listed in the sequence used in the original work; those enclosed in brackets were annotated by Delacour and Mayr (1945) as “aberrant.”

I. Subfamily Anserinae		II. Subfamily Anatinae						
1. Tribe Anserini	2. Tribe Dendrocygnini	1. Tribe Tadornini	2. Tribe Anatini	3. Tribe Aythiini	4. Tribe Cairinini	5. Tribe Mergini	6. Tribe Oxyurini	7. Tribe Merganettini
<i>Bramia</i>	<i>Dendrocygna</i>	<i>Lophonetta</i>	<i>Anas</i> ^a	<i>Netta</i>	<i>Amazonetta</i>	<i>Somateria</i> ^b	<i>Oxyura</i> ^c	<i>Merganetta</i>
<i>Anser</i>		<i>Tadorna</i>	[<i>Hymenolaimus</i>]	<i>Aythya</i>	<i>Chenonetta</i>	<i>Camptorhynchus</i>	<i>Biziura</i>	
<i>Cygnus</i>		<i>Alopochen</i>	[<i>Malacorhynchus</i>]		<i>Aix</i>	<i>Melanitta</i>	[<i>Thalassornis</i>]	
<i>Coscoroba</i>		<i>Neochen</i>	[<i>Rhodonessa</i>]		<i>Nettion</i>	<i>Histrionicus</i>	[<i>Heteronetta</i>]	
		<i>Cyanochen</i>	[<i>Stictonetta</i>]		<i>Sarkidiornis</i>	<i>Clangula</i>		
		<i>Chloephaga</i>			<i>Cairina</i> ^d	<i>Bucephala</i>		
		[<i>Cereopsis</i>]			<i>Plectropterus</i>	<i>Mergus</i> ^e		
		[<i>Tachyeres</i>]			[<i>Anseranas</i>]			

^a Includes *Salvadorina*, *Marmaronetta*, *Callonetta*, *Speculanas*, and *Mareca*.

^b Includes *Polysticta*.

^c Includes *Nomonyx*.

^d Includes *Pteronetta*

^e Includes *Mergellus* and *Lophodytes*.

anatomical and numerical characters were described, Verheyen (1953, 1955) proposed a novel classification of waterfowl. The idiosyncratic nature of the scheme by Verheyen (1953, 1955), in which the Anseriformes (exclusive of the screamers, Anhimae) were divided into four suborders (Anseres, Anseranates, Dendrocygnes, and Anates), 14 families (including monotypic Coscorobidae and Stictonettidae), and a number of tribes and informal groups, led to only a very limited acceptance by other systematists.

The utilization of osteological characters as a basis for the classification of waterfowl was advanced significantly by Woolfenden (1961). The summary classification proposed by Woolfenden (1961) largely followed that used by Delacour (1954, 1956, 1959), but with the following notable exceptions: *Anseranas* was segregated as a monotypic family; the swans (*Coscoroba*, *Cygnus*, and *Olor*), typical geese (*Anser* and *Branta*), and Cape Barren Goose were placed in separate tribes within the Anserinae; the Tribe Cairinini or "perching ducks" was dismantled, *Plectropterus* being assigned to the Tadornini and the remaining taxa to the Anatini; the eiders were returned to the seaducks (Mergini); and the aberrant *Rhodonessa* and *Merganetta* were moved from the Anatini to the Aythyini and the monotypic Merganettini, respectively.

The use of ethological phenetics for the estimation of the relationships of waterfowl became the primary focus of the research program of Johnsgard (1960a, 1961a, 1961b, 1962, 1965a, 1965b, 1968, 1978), and formed the basis for the second edition of Peter's "Checklist" by Johnsgard (1979). The classification of waterfowl presented in the "Checklist" did not include tribal taxa, but indicated most of the corresponding divisions at subfamilial rank and the sequence and content of genera agree with the earlier schemes by Johnsgard (1965a, 1978). Widely adopted classificatory revisions made by Johnsgard (1961a, 1965a, 1978, 1979) include: placement of *Thalassornis* as a close relative of *Dendrocygna*; inclusion of *Stictonetta* among the Anserinae; confirmation of the Tadorninae, including *Tachyeres*, as distinct from the true geese and other ducks; placement of *Marmaronetta* as transitional between dabbling ducks and pochards; and opposition to the removal of the eiders (*Somateria* and *Polysticta*) from the seaducks (Mergini) by Humphrey (1958) and Delacour (1959). The systematic assessments by Johnsgard, like those of Delacour and Mayr (1945) and Delacour (1954, 1956, 1959), also considered capacity for interspecific hybridization to be indicative of close phylogenetic relationship (e.g., Johnsgard, 1960b, 1968; Gillham and Gillham, 1996). The study of interspecific hybrids in waterfowl has a long history (e.g., Phillips, 1915, 1928; Sibley, 1957; Johnsgard, 1960b, 1963; Scherer and Hilsberg, 1982), and the view that loss of capacity for hybridization is critical to speciation is related to the "recognition concept" of species (McEvey, 1993; Lambert and Spencer, 1995).

Brodkorb (1964) and Howard (1964) independently provided comprehensive, taxonomically arranged listings of fossil waterfowl. An original contribution to the systematics of waterfowl was the classification by Wolters (1976), one marked by narrowly delimited genera and an unusual attention to lesser taxonomic ranks. The classification by Delacour and Mayr (1945), as revised by Delacour (1954, 1956, 1959) and Johnsgard (1965a, 1978, 1979), was adopted with few or no refinements by Blake (1977), Cramp and Simmons (1977), Todd (1979, 1996), Brown et al. (1982), the American Ornithologists' Union (1983), Marchant and Higgins (1990), and Carboneras (1992). The tradition of phenetic comparisons of behavioral patterns as a basis for the systematics of waterfowl continues to the

present day (e.g., Eldridge, 1979, 1985; Fullagar and Carbonell, 1986; Fullagar et al., 1990; Young, 1995), in spite of the advantages of applying phylogenetic methods for behavior-based reconstructions (de Queiroz and Wimberger, 1993; Wimberger and de Queiroz, 1996).

Classifications Based on Molecular Studies.—The first biochemically based assessments of the relationships of Anseriformes were not phylogenetic (sensu cladistic), and pose the same methodological difficulties as intuitive reconstructions based on comparative behavior. Regardless of the analytical details—including underlying data, metrics employed, presentation of dendrograms, or partial agreement among phenetic arrangements or between phenograms and phylogenetic trees (Scherer and Sontag, 1986; Bledsoe and Raikow, 1990)—patterns of overall similarity (or dissimilarity) are not reliable estimators of phylogenetic relationships (Wiley, 1981). Nonphylogenetic, molecular comparisons involving waterfowl include: qualitative comparisons of proteins (Sibley, 1960; Sibley and Ahlquist, 1972; Brush, 1976), immunological comparisons (Bottjer, 1983), phenetic studies based on electrophoresis (Numachi et al., 1983; Patton and Avise, 1985; Oates and Principato, 1994), quantitative phenetics of uropygial lipids (Jacob and Glaser, 1975; Jacob, 1982; Jacob and Hoerschelmann, 1993), and restriction-site analysis of mitochondrial and nuclear DNA (Kessler and Avise, 1984, 1985; Tuohy et al., 1992). Although generalizations about these studies are problematic because of the diversity of methodologies and taxonomic representations upon which the inferences were based, several consistent patterns emerged (reviewed by Scherer and Sontag, 1986): *Anseranas* is markedly distinct from other waterfowl, swans and true geese are more similar to each other than to other anatids, and the true ducks (Anatini, Aythyini, Mergini, and Oxyurini) tend to be more similar to each other than to other anatids.

The most widely publicized DNA-based research program to date was that by Sibley and colleagues, using DNA hybridization (Sibley and Ahlquist, 1990). Unfortunately, this technique, like those summarized above, is phenetic and therefore subject to groupings distorted by autapomorphy, unequal rates of evolution, sympleisiomorphy, or (as with any method of reconstruction) homoplasy (Cracraft, 1987a; Houde, 1987; Sarich et al., 1989; Springer and Krajewski, 1989; Sheldon and Bledsoe, 1993). Assertions that DNA hybridization, properly applied, can provide distance measures that transcend the inherent analytical shortcomings of phenetic estimates (e.g., Bledsoe and Sheldon, 1990; Sheldon, 1994; Sheldon et al., 1995) have not been substantiated. In addition, the application of this technique by Sibley and Ahlquist (1990) was criticized on other methodological grounds, including sparse data matrices, unspecified transformations of data, and suboptimal clustering algorithms (Lewin, 1988a, 1988b; Cracraft, 1992a; Lanyon, 1992; Mindell, 1992).

Classifications stemming from this work (Sibley et al., 1988; Sibley and Monroe, 1990, 1993) were based only loosely on the published trees (Siegel-Causey, 1993), and those for the Anseriformes were extended far beyond the 13 species (representing *Anhima*, *Chauna*, *Anseranas*, *Dendrocygna*, *Branta*, *Cygnus*, *Aix*, *Anas*, *Melanitta*, and *Oxyura*) actually sampled by Sibley and Ahlquist (1990). Consequently, several unusual aspects of their proposed classification—including the merging of true geese, sheldgeese, shelducks, and some “perching” ducks in the single Tribe Anserini, or the inclusion of pochards and seaducks with dabbling ducks in the Tribe Anatini—were made without justification. The basis for the classification by Sibley and Monroe (1990) is undermined further by the subjective placements of most of the sampled taxa within the trees, necessitated by the sparsity of the distance matrix and the

asymmetry of comparisons; these empirically unsupported placements include those for *Dendrocygna*, *Branta*, *Cygnus*, and *Oxyura* (Lanyon, 1992). The supplement prepared by Sibley and Monroe (1993) included only two important classificatory revisions for the waterfowl: adoption of the taxonomic sequence for the Anatini proposed by Livezey (1991), and return of *Heteronetta* to the stiff-tailed ducks.

Reanalysis of the data compiled by Sibley and Ahlquist (1990) by Harshman (1994) confirmed only the basal position of *Anseranas* with respect to other waterfowl. A concurrent study using DNA hybridization by Madsen et al. (1988) suffered from comparable limitations of taxonomic sampling as well as unfavorable properties of summary metrics; the analysis indicated patterns of similarity largely congruent with traditional perceptions of relationships, with the exception of a comparatively basal placement of *Oxyura*, an inference shared by Sibley and Ahlquist (1990).

To date, the only published cladistic reconstructions of relationships of waterfowl using molecular data are those by Sraml et al. (1996) and Mindell et al. (1997); the first of these studies was based on sequence data from cytochrome *b* and the second from 12S rDNA. The study by Sraml et al. (1996) was severely limited both with respect to the taxa included and the sampling of the gene; the latter deficiency underlies the poor support of nodes in the resultant trees. The reconstruction by Mindell et al. (1997), to the extent possible given the limited number of anseriform taxa represented, is consistent with that presented here (Fig. 1) with the exception of the placement of *Anseranas* as the sister group of the Anhimidae; counter evidence for the latter grouping is presented by Livezey (1997b).

An ongoing analysis by Harshman (personal communication) using cytochrome *b* represents a significant improvement in both taxonomic and genomic sampling, and preliminary indications are that greater resolution and support of nodes was achieved. The relationships indicated in the analysis by Harshman (personal communication) contrast markedly with the poorly resolved groupings suggested by Sraml et al. (1996) and show substantial agreement with those proposed by Livezey (1986a) and Mindell et al. (1997). Reconstructions by Harshman (personal communication) that differ from those summarized in this classification include: the position of *Coscoroba* and *Cereopsis* as sister genera; the Oxyurini as sister group to the Tadorninae and Anatinae (the latter groups being merged); and unexpected difficulties in topological placements of *Nettapus*, some *Cairina*, and the bizarre *Biziura*.

The provision of sequence data for a number of Anseriformes and outgroups (Galliformes) makes possible the direct comparison of comparable phylogenetic (cladistic) hypotheses based on independent morphological and molecular data, and hopefully will contribute toward a consensus concerning the relative merit of congruence across analyses, trees based on combined data, and attendant issues of character weighting (morphological versus molecular characters, transversions versus transitions in sequence data), rooting of trees, and the statistical attributes of diverse types of data (Neff, 1986; Wheeler, 1986; Sanderson and Donoghue, 1989; Swofford, 1991; Chippindale and Wiens, 1994; Omland, 1994; de Queiroz et al., 1995; Hillis et al., 1996). Only with empirical assessments of this kind can systematics move away from speculation and prejudice (e.g., Sibley and Ahlquist, 1987, 1990; Monroe, 1989; Hedges and Sibley, 1994; Sibley, 1994) and toward reconstructive methods and hypotheses that incorporate the maximal phylogenetic information from all available data (Hillis, 1987; Cracraft and Mindell, 1989; Moritz and Hillis, 1990; Eernisse and Kluge, 1993; Patterson et al., 1993; Avise, 1996; Hillis et al., 1996).

Fig. 1.—Tree summarizing the phylogenetic relationships among genera of Anseriformes reflected in the proposed classification; half-tone lines indicate provisional groupings or placements. Analyses upon which the classification is based include the original genus-level analysis of the order (Livezey, 1986a), as well as works specific to included subgroups (most to species level), indicated by circled numbers by corresponding nodes in the tree: (1) Livezey (1997a); (2) Livezey (1989a, 1996a); (3) Livezey (1995a); (4) Livezey (1996a); (5) Livezey (1986b, 1986c, 1989a, 1996b); (6) Livezey (1997a); (7) Livezey (1995b); (8) Livezey (1990, 1991, 1993a, 1996b); (9) Livezey (1996c); and (10) Livezey (1989b, 1993b, 1995c).

Proposed Phylogenetic Classification

General Objectives.—The primary objective of this paper is to summarize in a single classification the findings of a series of works on the systematics of Recent Anseriformes (Livezey, 1986a, 1986b, 1986c, 1989a, 1989b, 1990, 1991, 1993a, 1993b, 1995a, 1995b, 1995c, 1996a, 1996b, 1996c, 1997a, 1997b) using phylogenetic (cladistic) methods (Hennig, 1966; Wiley, 1981). A graphical summary of the genus-level phylogenetic inferences of these works is depicted in Figure 1. This classification is proposed in the hope that it will provide a constructive, evolutionary framework for the study of waterfowl, an aspiration contrary to the conservative view in which “standard taxonomic sequences” are to be insulated from classificatory revisions (Mayr, 1989; Bock, 1990; Mayr and Bock, 1994). The notion that stability of taxonomic sequences is of greater importance than the communication of current opinions on phylogeny, combined with an abiding pessimism regarding the likelihood of accurate phylogenetic reconstructions or classifications, reached an extreme in the recommendation that ornithologists adopt an alphabetical sequence of taxa (species within genera, genera within subfamilies, and so on) as a global standard (Moreau, 1961; Lack, 1967, 1968). Ironically, the proposed imposition of stability on the dynamic changes in accepted systematic relationships would exacerbate the mistaken notion that the phylogeny of the Class Aves is well known (e.g., Ricklefs, 1980).

Revisions and Corrections.—This classification incorporates a number of changes in phylogenetic inferences made since the original, preliminary work by Livezey (1986a), together with changes since Livezey (1989a). In addition, this final synthesis is updated by provisional species-level revisions of several problematic modern genera of waterfowl (e.g., *Sarkidiornis*, *Merganetta*), discussions of taxonomically vexing “species groups” (e.g., *Branta canadensis*), and preliminary placements of well-represented fossil taxa. Also included are two decisions subsequent to earlier phylogenetic works on the groups concerned (Livezey, 1996b, 1997a) to elevate taxa from subgeneric to generic rank (*Casarca*, *Aristonetta*), to better represent inferred phylogenetic relationships in the classification. This summary classification also incorporates the correction of several errors of authorship in preceeding classifications (Livezey, 1995b, 1995c, 1996b, 1996c; Table 2) and generic seniority (Livezey, 1996c), clarifies adoption of subgenera of *Dendrocygna* under the principle of first reviser (Livezey, 1995a), and coordinates subtribal names in accordance with the recommendations of the International Commission on Zoological Nomenclature (1985).

METHODS

Phylogenetic Classification

The construction of classifications based on explicit phylogenetic hypotheses follows the principles outlined by Wiley (1981), with the exception that normal taxa are used for fossils and annotated by a dagger (†), as opposed to the use of “plesion.” The dagger is restricted to fossil taxa (i.e., extinct forms known only from subfossil and fossil remains), and is not used to indicate species extirpated in modern times (e.g., *Camptorhynchus labradorius*). These conventions include the use of sequencing three or more taxa of the same rank (in order of increasing close relationship) within a single higher taxon to avoid the unwieldy proliferation of ranks to maintain a strictly dichotomous classificatory scheme. Where such sequences of taxa of equal rank are of indeterminate relationship, the defining,

Table 2.—*Compilation of modern family-group taxa used in the proposed classification and corresponding authors, with comparison of original ranks of these group names and the first use of these names at the rank used in the present work.*

Current family-group taxon	Author of senior family-group taxon	Original rank of senior family-group taxon	First designation of taxon at current taxonomic rank
Superfamily Anseranatoidea	Sclater, 1880	Subfamily	Sibley et al., 1988
Superfamily Anatoidea	Leach, 1829	Family	Livezey, 1997 <i>b</i>
Family Anhimidae	Stejneger, 1885	Family	—
Family Anseranatidae	Sclater, 1880	Subfamily	Stejneger, 1885
Family Anatidae	Leach, 1829	Family	—
Subfamily Dendrocygninae	Reichenbach, 1849–1850	Family	—
Subfamily Anserinae	Vigors, 1825 <i>b</i>	Subfamily	—
Subfamily Stictonettinae	Boetticher, 1950	Subtribe ^a	Wolters, 1976
Subfamily Tadorninae	Reichenbach, 1849–1850	Subfamily	—
Subfamily Anatinae	Leach, 1820	Family	Swainson, 1837
Tribe Dendrocygnini	Reichenbach, 1849–1850	Family	Delacour and Mayr, 1945
Tribe Thalassornithini	Livezey, 1986	Subfamily ^b	Livezey, 1995 <i>a</i>
Tribe Cereopsini	Vigors, 1825 <i>b</i>	Subfamily	Boetticher, 1942
Tribe Anserini	Vigors, 1825 <i>b</i>	Subfamily	Delacour and Mayr, 1945
Tribe Cygnini	Vigors, 1825 <i>b</i>	Subfamily	Delacour and Mayr, 1945
Tribe Merganettini	Bonaparte, 1853	Subfamily ^c	Delacour and Mayr, 1945
Tribe Plectropterini	Eyton, 1838	Subfamily	Livezey, 1996 <i>b</i>
Tribe Tadornini	Reichenbach, 1849–1850	Subfamily	Delacour and Mayr, 1945
Tribe Malacorhynchini	Boetticher, 1950	Tribe ^a	—
Tribe Anatini	Leach, 1820	Family	Delacour and Mayr, 1945
Tribe Aythyini	Delacour and Mayr, 1945	Tribe	—
Tribe Mergini	Rafinesque, 1815; or Swainson, 1831	Subfamily	Delacour and Mayr, 1945
Tribe Oxyurini	Phillips, 1926	Subfamily	Delacour and Mayr, 1945
Subtribe Coscorobina	Boetticher, 1936–1938	Subfamily	Boetticher, 1952 ^a
Subtribe Cygnina	Vigors, 1825 <i>b</i>	Subfamily	Boetticher, 1952 ^e
Subtribe Chloephagina	Boetticher, 1942	Tribe ^a	Boetticher, 1952 ^a
Subtribe Tadornina	Reichenbach, 1849–1850	Subfamily	Boetticher, 1952 ^a
Subtribe Cairinina	Boetticher, 1936–1938	Subfamily ^a	Boetticher, 1952 ^{a,d,e}
Subtribe Nettapodina	Bonaparte, 1856	Subfamily ^a	Livezey, 1991 ^d
Subtribe Anatina	Leach, 1820	Family	Boetticher, 1952 ^e
Subtribe Marmaronettina	Livezey, 1996	Subtribe ^c	—
Subtribe Rhodonessina	Boetticher, 1950	Tribe ^a	Boetticher, 1952 ^e
Subtribe Aythyina	Delacour and Mayr, 1945	Tribe	Boetticher, 1952 ^e
Subtribe Somaterina	Reichenbach, 1849–1850	Subfamily	Boetticher, 1952 ^e
Subtribe Mergina	Rafinesque, 1815; or Swainson, 1831	Subfamily	Boetticher, 1952 ^e
Subtribe Heteronettina	Boetticher, 1950	Tribe ^a	Boetticher, 1952 ^e
Subtribe Oxyurina	Phillips, 1926	Subfamily	Boetticher, 1952 ^e

^a Taxa given “section” endings of *-ae*, conventional for botanical tribe; Bonaparte (1853, 1856), Boetticher (1942), and Boetticher (1950) treated these as equivalent to tribes (i.e., as primary subdivisions of subfamilies), but Boetticher (1952) later explicitly treated these as partitions of tribes.

^b Original derivation of subfamily (Thalassorninae) incorrect; emended by Livezey (1989*a*).

^c Originally used as subfamily of Family Erismaturidae, comprising *Merganetta* and the stiff-tailed ducks, therefore approximately equivalent to a tribe in the current sense.

^d First treated at tribal rank (Cairinini) by Delacour and Mayr (1945).

^e Original ending of *-ae* retained by Livezey (1991, 1995*b*), coordinated herein with conventional ending of *-ina* for subtribes.

next-higher taxon is annotated *sedis mutabilis*; where groups of taxa are of uncertain monophyly, the defining taxon is annotated *incertae sedis*. Higher-order taxa were based largely on published synonymies and classifications (Boetticher, 1942, 1950, 1952; Brodkorb, 1964; Wolters, 1976; Bock, 1994). Within the limits of these conventions, the classification was constructed to: (1) conform with existing nomenclatural codes for availability and seniority of taxa; (2) reflect the maximal number of hierarchical ranks and areas of uncertainty inferred in the companion phylogenetic analyses; and (3) avoid, where content-neutral, the proposal of new ranks or binomial combinations. Complete literature references are not provided for each author-year citation given for taxa in the classification, but instead are limited to direct citations of publications in the narrative parts of the text, as well as in tables, figure legends, and appendices. The English name for a higher taxon is not given where this simply would repeat that of the next-lower, included taxon.

Species Limits

The identification of the working units in phylogenetic analyses, i.e., the delimitation of species, is a critical and problematic part of any systematic study. The prospects of achieving a species-level classification satisfactory to all is as unlikely for the Anseriformes as for any vertebrate order. The controversy and conflicting paradigms that attend such taxonomic decisions in waterfowl is exemplified by the continuing controversy involving the species-level delimitations within the mallard (*Anas platyrhynchos*) group (Yamashina, 1948; Johnsgard, 1961c, 1967; Aldrich and Baer, 1970; Williams and Roderick, 1973; Heusmann, 1974; Braithwaite and Miller, 1975; Morgan et al., 1976; Hubbard, 1977; Brodsky and Weatherhead, 1984; Haddon, 1984; Gillespie, 1985; Ankney et al., 1986, 1987; Ankney and Dennis, 1988; Bélanger et al., 1988; Brodsky et al., 1988; Hepp et al., 1988; Avise et al., 1990; Hitchmough et al., 1990; Livezey, 1991, 1993a; Browne et al., 1993; Reichel and Lemke, 1994; Rhymer et al., 1994).

In this work, the Anseriformes are classified to species level, with included subspecies indicated for polytypic species. In delimiting species-level taxa, my approach is simply to distinguish the terminal taxa that differ in at least one of the characters analyzed. This practice represents a practical application of the phylogenetic species concept in the context of morphological characters (Cracraft, 1983, 1987b, 1988, 1992b, McKittrick and Zink, 1988; Nixon and Wheeler, 1990; Davis and Nixon, 1992; Zink and McKittrick, 1995), which approximates in many such cases the lineages that are distinguished under the evolutionary species concept (Wiley, 1978; Frost and Hillis, 1990; Frost and Kluge, 1994). In some cases these terminal taxa correspond to conventional subspecies (e.g., within *Somateria mollissima*), whereas in others the working taxa include two or more recognized subspecies (e.g., even a narrowly delimited *Anas platyrhynchos* includes *conboschas*). However, this analytical extrapolation does not necessarily represent a recommendation to the ornithological community at large or the bird-watching public that these lineages be elevated uncritically to species status in checklists, field guides, and popular books. Instead, recognition of taxa at species rank in this classification represents a compromise based primarily on the practicalities of phylogenetic reconstruction and secondarily on the goal of conserving taxonomically the maximal amount of demonstrated evolutionary divergence between sister lineages. Characters used in provisionally delimiting taxa within species groups

not subjected to formal analysis in previous works (*Branta canadensis*, *Sarkidiornis melanotos*, and *Merganetta armata*) are given in the Appendix.

Fossil Taxa

In spite of persistent methodological shortcomings of many paleornithological reconstructions (see general critiques by Cracraft, 1979, 1980), paleontological finds continue to offer significant new insights into the phylogeny and biogeography of waterfowl. Paleontologically facilitated advances in our understanding of waterfowl include an enhanced appreciation of insular endemism (Olson and James, 1991), one likely to undergo further refinements with continued study of subfossil anseriforms in New Zealand (P. R. Millener, personal communication), Madagascar (S. M. Goodman, personal communication), and smaller Pacific islands (cf. Derscheid, 1939), as well as the paleontological documentation of former continental distributions of modern tribes (e.g., Nearctic tadornines; Ross, 1935; Brodkorb, 1964; Howard, 1964). Consequently, an effort was made to include well-represented fossil anseriforms in the classification, either on the basis of formal phylogenetic analyses (e.g., Livezey and Martin, 1988; Livezey, 1989a, 1996a, 1997b) or on diagnoses based on synapomorphies inferred from analyses of modern representatives (Livezey, 1986a, 1986b, 1986c, 1989a, 1989b, 1990, 1991, 1993a, 1993b, 1995a, 1995b, 1995c, 1996a, 1996b, 1996c, 1997a, 1997b).

A number of fossil taxa, however, lacked material adequate for phylogenetic assignment and were omitted from the classification, including: *Paranyroca magna* (Miller and Compton, 1939), *Romainvillia stehlini* (Lebedinsky, 1927), *Eonesasa anaticula* (Wetmore, 1938), *Cygnopterus affinis* (Van Beneden, 1883), *Cygnopterus alphonsi* (Cheneval, 1984), *Cygnavus senckenbergi* (Lambrecht, 1931), *Cygnanser csakvarensis* (Lambrecht, 1933), *Paracygnus plattensis* (Short, 1969), *Presbychen abavus* (Wetmore, 1930), *Heterochen pratensis* (Short, 1970), *Eremochen russelli* (Brodkorb, 1961), *Brantadorna robusta* (Short, 1970), *Ocyplonessa shotwelli* (Brodkorb, 1961), and *Aldabranas cabri* (Harrison and Walker, 1978). Also excluded are a number of fossil taxa assigned to *Dendrocygna*, *Anser*, *Branta*, *Cygnus*, *Anas*, and *Aythya*, most of which are inadequately represented for confident assignment to genus (Brodkorb, 1964; Howard, 1964), although published descriptions indicate that some excluded taxa classified as *Branta* or *Cygnus* may be accurate at least to tribal level.

An indication of the poor diagnosability of European fossils assigned to anseriform genera during the late 19th and early 20th centuries is provided by Mlíkovský (1992), in which 13 fossil anseriform taxa were reclassified as follows: Aves, incertae sedis (two); families in orders other than the Anseriformes (two); Anseriformes, incertae sedis (one); Anatidae, incertae sedis (one); Aythyini, incertae sedis (one); referral to a genus in another tribe of Anatidae, some merely confirming earlier reclassifications by others (four); referral to a genus in the same tribe of Anatidae (one); and retention in the original genus (one). Most assignments of fossils from the Oligocene or Miocene to modern genera (e.g., *Anas* and *Aythya*) probably represent misclassifications of at least subfamilial scale (Brodkorb, 1962; Livezey and Martin, 1988). Some taxa assigned to *Cygnus* (Northcote, 1982, 1988, 1992) and "*Anas*" (Newton and Gadow, 1893; Wetmore, 1960; Olson and Jouventin, 1996) were represented by sufficient material for approximate placements. Several taxa of fossil ducks from Australia were synonymized with modern species by Olson (1977a), whereas the validity and generic assignments

of two distinctive New Zealand fossil taxa were confirmed (Olson, 1977*b*). The position of "*Mergus*" *miscellus* described by Alvarez and Olson (1978), if inclusion within the *Mergini* is justified, remains unclear and the taxon is not included in this classification (Livezey and Martin, 1988).

PHYLOGENETIC CLASSIFICATION OF ANSERIFORMES

Superorder Galloanserimorphae (Sibley et al., 1988).—Fowl

Order Anseriformes (Wagler, 1831).—Waterfowl

Suborder Anhimae Wetmore and Miller, 1926

Family Anhimidae Stejneger, 1885.—Screamers

Genus *Anhima* Brisson, 1760

Anhima cornuta (Linnaeus, 1766).—Horned Screamer

Genus *Chauna* Illiger, 1811.—Crested screamers

Chauna chavaria (Linnaeus, 1766).—Northern Crested Screamer

Chauna torquata (Oken, 1816).—Southern Crested Screamer

Suborder Anseres Wagler, 1831.—True waterfowl

Superfamily Anseranatoidea (Sclater, 1880)

Family Anseranatidae (Sclater, 1880)

Genus *Anseranas* Lesson, 1828

Anseranas semipalmata (Latham, 1798).—Magpie Goose

Superfamily Anatoidea (Leach, 1820).—True waterfowl

†**Family Presbyornithidae** Wetmore, 1926

Genus *Presbyornis* Wetmore, 1926

Presbyornis pervetus Wetmore, 1926

†**Family Cnemiornithidae** Stejneger, 1885

Genus *Cnemiornis* Owen, 1865.—New Zealand geese

Cnemiornis calcitrans Owen, 1866.—South Island Goose

Cnemiornis gracilis Forbes, 1892.—North Island Goose

Family Anatidae Leach, 1820.—Typical waterfowl

Subfamily Dendrocygninae Reichenbach, 1849–1850.—Whistling-ducks and allies

Tribe Dendrocygnini (Reichenbach, 1849–1850).—Whistling-ducks

Genus *Dendrocygna* Swainson, 1837^a

Subgenus *Lamprocygna* Boetticher, 1949

Dendrocygna viduata (Linnaeus, 1766).—White-faced Whistling-Duck

Dendrocygna autumnalis (Linnaeus, 1758).—Black-bellied Whistling-Duck (includes *fulgens* Friedmann, 1947)

Subgenus *Dendrocygna* Swainson, 1837

Infragenus *Nesocygna* Boetticher, 1949

Dendrocygna guttata Schlegel, 1866.—Spotted Whistling-Duck

Dendrocygna arborea (Linnaeus, 1758).—West Indian Whistling-Duck

Infragenus *Dendrocygna* Swainson, 1837; sedis mutabilis

Dendrocygna bicolor (Vieillot, 1816).—Fulvous Whistling-Duck

Dendrocygna eytoni (Eyton, 1838).—Plumed Whistling-Duck

Dendrocygna arcuata (Horsfield, 1824).—Wandering Whistling-Duck (includes *australis* Reichenbach, 1849–1850; and *pygmaea* Mayr, 1945)

Dendrocygna javanica (Horsfield, 1821).—Lesser Whistling-Duck

Tribe Thalassornithini (Livezey, 1986)

Genus *Thalassornis* Eyton, 1838

Thalassornis leuconotus Eyton, 1838.—White-backed Duck (includes *insularis* Richmond, 1897)

†**Subfamily Dendrocheninae** Livezey and Martin, 1988

Genus *Dendrochen* Miller, 1944

Dendrochen robusta Miller, 1944

Genus *Mionetta* Livezey and Martin, 1988^b

Mionetta blanchardi (Milne-Edwards, 1863)

Subfamily Anserinae Vigors, 1825.—Geese and swans

Tribe Cereopsini (Vigors, 1825)

Genus *Cereopsis* Latham, 1801

Cereopsis novaehollandiae Latham, 1801.—Cape Barren Goose

Tribe Anserini (Vigors, 1825).—True geese; sedis mutabilis

Genus *Anser* Brisson, 1760.—Pale-breasted geese

Subgenus *Anser* Brisson, 1760

Anser cygnoides (Linnaeus, 1758).—Swan Goose

Anser fabalis (Latham, 1787).—Bean Goose^c

Anser (f.) *fabalis* (Latham, 1787).—Taiga Bean Goose (includes *middendorffii* Severtsov, 1873; and *johanseni* Delacour, 1951)

Anser (f.) *serrirostris* Swinhoe, 1871.—Tundra Bean Goose (includes *rossicus* Buturlin, 1933)

Anser brachyrhynchus Baillon, 1834.—Pink-footed Goose

Anser anser (Linnaeus, 1758).—Greylag Geese

Anser (a.) *anser* (Linnaeus, 1758).—Western Greylag Goose

Anser (a.) *rubrirostris* Swinhoe, 1871.—Eastern Greylag Goose

Anser albifrons (Scopoli, 1769).—Greater White-

fronted Goose (includes *gambeli* Hartlaub, 1852; *frontalis* Baird, 1858; *flavirostris* Dalgely and Scott, 1948; and *elgasi* Delacour and Ripley, 1975)

Anser erythropus (Linnaeus, 1758).—Lesser White-fronted Goose

Subgenus *Chen* Boie, 1822

Anser indicus (Latham, 1790).—Bar-headed Goose

Anser canagicus (Sevastianov, 1802).—Emperor Goose

Anser caerulescens (Linnaeus, 1758).—Snow Goose (includes *atlanticus* [Kennard, 1927])

Anser rossii Cassin, 1861.—Ross's Goose

†Genus *Geochen* Wetmore, 1943^d

Geochen rhuax Wetmore, 1943.—Large Hawaiian Goose

Genus *Branta* Scopoli, 1769.—Brant (dark-breasted) geese

Subgenus *Leucoblepharon* Baird, 1858; sedis mutabilis

Branta canadensis-group (Linnaeus, 1758); sedis mutabilis.—Canada Goose^e

Branta (c.) *canadensis* (Linnaeus, 1758).—Atlantic Canada Goose (includes *interior* Todd, 1938)

Branta (c.) *moffitti* Aldrich, 1946.—Giant Canada Goose (includes *maxima* Delacour, 1951)

Branta (c.) *leucopareia* Brandt, 1836.—Aleutian Canada Goose (includes *asiatica* Aldrich, 1946)

Branta (c.) *hutchinsii* (Richardson, 1832).—Lesser Canada Goose (includes *parvipes* [Cassin, 1852])

Branta (c.) *occidentalis* (Baird, 1858).—Dusky Canada Goose (includes *fulva* Delacour, 1951)

Branta (c.) *minima* Ridgway, 1885.—Cackling Canada Goose (includes *taverneri* Delacour, 1951)

†*Branta hylobadistes* Olson and James, 1991.—Greater Nene

Branta sandvicensis (Vigors, 1834).—Lesser Nene

Subgenus *Branta* Scopoli, 1769

Branta bernicla (Linnaeus, 1758).—Dark-bellied Brant (includes *nigricans* [Lawrence, 1846]; and *orientalis* Tugarinov, 1941)

Branta hrota (Müller, 1776).—Pale-bellied Brant

Subgenus *Leucopareia* Reichenbach, 1853

Branta leucopsis (Bechstein, 1803).—Barnacle Goose

Branta ruficollis (Pallas, 1769).—Red-breasted Goose

Tribe Cygnini (Vigors, 1825).—Swans

Subtribe Coscorobina (Boetticher, 1936–1938)

Genus *Coscoroba* Reichenbach, 1853

Coscoroba coscoroba (Molina, 1782).—Coscoroba Swan

Subtribe Cygnina (Vigors, 1825).—Typical swans

Genus *Cygnus* Bechstein, 1803^f

Subgenus *Chenopsis* Wagler, 1823.—Austral swans

Cygnus atratus (Latham, 1790).—Black Swan

†*Cygnus sumnerensis* (Forbes, 1890).—New Zealand Swan^g

Cygnus melanocoryphus (Molina, 1782).—Black-necked Swan

Subgenus *Cygnus* Bechstein, 1803

Cygnus olor (Gmelin, 1789).—Mute Swan

†*Cygnus equitum* Bate, 1916.—Dwarf Maltese Swan

Subgenus *Olor* Wagler, 1832.—Tundra swans

†*Cygnus falconeri* Parker, 1865.—Giant Maltese Swan

Cygnus buccinator (Richardson, 1831).—Trumpeter Swan

Cygnus columbianus (Ord, 1815).—Whistling Swan

Cygnus bewickii (Yarrell, 1830).—Bewick's Swan

Cygnus cygnus (Linnaeus, 1758).—Whooper Swan

†**Tribe Thambetochenini** Livezey, 1996.—Moa-nalos^h

Genus *Chelychelynechen* Olson and James, 1991

Chelychelynechen quassus Olson and James, 1991.—Turtle-billed Moa-nalo

Genus *Ptaiochen* Olson and James, 1991

Ptaiochen pau Olson and James, 1991.—Short-billed Moa-nalo

Genus *Thambetochen* Olson and Wetmore, 1976

Thambetochen chauliodus Olson and Wetmore, 1976.—Greater Moa-nalo

Thambetochen xanion Olson and James, 1991.—Oahu Moa-nalo

Subfamily Stictonettinae (Boetticher, 1950)

Genus *Stictonetta* Reichenbach, 1853

Stictonetta naevosa (Gould, 1841).—Freckled Duck

Subfamily Tadorninae Reichenbach, 1849–1850.—Shelducks and allies

Tribe Merganettini (Bonaparte, 1853).—Torrent-ducks and allies

Genus *Hymenolaimus* Gray, 1843

Hymenolaimus malacorhynchus (Gmelin, 1789).—Blue Duck

Genus *Tachyeres* Owen, 1875.—Steamer-ducksⁱ

Tachyeres patachonicus (King, 1831).—Flying Steamer-Duck

Tachyeres pteneres (Forster, 1844).—Magellanic Flightless Steamer-Duck

Tachyeres brachypterus (Latham, 1790).—Falkland Flightless Steamer-Duck

Tachyeres leucocephalus Humphrey and Thompson, 1981.—White-headed Flightless Steamer-Duck
 Genus *Merganetta* Gould, 1842.—Torrent-ducks
Merganetta armata-group Gould, 1841; sedis mutabilis^j

Merganetta (m.) *armata* Gould, 1841.—Southern Torrent-Duck

Merganetta (m.) *turneri* Sclater and Salvin, 1869.—Turner's Torrent-Duck

Merganetta (m.) *garleppi* Berlepsch, 1894.—Bolivian Torrent-Duck (includes *berlepschi* Hartert, 1909)

Merganetta (m.) *leucogenis* (Tschudi, 1843).—Peruvian Torrent-Duck

Merganetta (m.) *colombiana* Des Murs, 1845.—Colombian Torrent-Duck

Tribe Plectropterini (Eyton, 1838).—Pied shelducks

Genus *Plectropterus* Stephens, 1824

Plectropterus gambensis (Linnaeus, 1766).—Spur-winged Goose (includes *niger* Sclater, 1877)

Genus *Sarkidiornis* Eyton, 1838.—Comb-ducks^k

Sarkidiornis melanotos (Pennant, 1769).—Gray-sided Comb-Duck

Sarkidiornis sylvicola Ihering and Ihering, 1907.—Black-sided Comb-Duck

†**Tribe Euryanatini** (Livezey, 1989)^l

Genus *Eurynas* Oliver, 1930

Eurynas finschi (Van Beneden, 1875).—Finsch's Duck

Tribe Tadornini (Reichenbach, 1849–1850).—True shelducks and sheldgeese

Subtribe indeterminate^m

†Genus *Centronis* Andrews, 1897

Centronis majori Andrews, 1897.—Greater Madagascan Sheldgoose

†Genus *Anabernicula* Ross, 1935.—Pygmy sheldgeese

Anabernicula minuscula Wetmore, 1924

Anabernicula gracilentia Ross, 1935

Anabernicula oregonensis Howard, 1964

Subtribe Chloephagina (Boetticher, 1942).—Sheldgeese

Genus *Cyanochen* Bonaparte, 1856

Cyanochen cyanopterus (Rüppell, 1845).—Blue-winged Sheldgoose

Genus *Alopochen* Stejneger, 1885ⁿ; sedis mutabilis

Alopochen aegyptiacus (Linnaeus, 1766).—African Sheldgoose

†*Alopochen sirabensis* (Andrews, 1897).—Lesser Madagascan Sheldgoose^o

†*Alopochen mauritianus* (Newton and Gadow, 1893).—Mauritius Sheldgoose^o

- Genus *Neochen* Oberholser, 1918
Neochen jubata (Spix, 1825).—Orinoco Sheldgoose
†*Neochen pugil* (Winge, 1887).—Greater Orinoco Sheldgoose °
- Genus *Chloephaga* Eyton, 1838.—Neotropical sheldgeese
Subgenus *Oressochen* Bannister, 1870
Chloephaga melanoptera (Eyton, 1838).—Andean Sheldgoose
- Subgenus *Chloephaga* Eyton, 1838.—Patagonian sheldgeese; sedis mutabilis
Infragenus *Chloephaga* Eyton, 1838
Chloephaga picta (Gmelin, 1789).—Upland Sheldgoose (includes *leucoptera* [Gmelin, 1789])
- Infragenus *Taenidiestes* Reichenbach, 1853
Chloephaga hybrida (Molina, 1782).—Kelp Sheldgoose (includes *malvinarum* Phillips, 1916)
- Infragenus *Chloetrophus* Bannister, 1870.—Hooded sheldgeese
Chloephaga poliocephalus Sclater, 1857.—Ashy-headed Sheldgoose
Chloephaga rubidiceps Sclater, 1860.—Ruddy-headed Sheldgoose
- Subtribe Tadornina** (Reichenbach, 1849–1850).—Shelducks
†Genus *Pachyanas* Oliver, 1955 ^m
Pachyanas chathamica Oliver, 1955.—Chatham Island Shelduck
- Genus *Tadorna* Oken, 1817.—Banded shelducks
Tadorna tadorna (Linnaeus, 1758).—Red-billed Shelduck
Tadorna radjah (Lesson, 1828).—Radjah Shelduck (includes *rufitergum* Hartert, 1905)
- Genus *Casarca* Bonaparte, 1838.—Unbanded shelducks
Subgenus *Casarca* Bonaparte, 1838.—Reddish shelducks
Casarca ferruginea (Pallas, 1764).—Ruddy Shelduck
Casarca cana (Gmelin, 1789).—Cape Shelduck
- Subgenus *Pseudotadorna* Kuroda, 1917.—Blackish shelducks
Casarca tadornoides (Jardine and Selby, 1828).—Australian Shelduck
Casarca variegata (Gmelin, 1789).—Paradise Shelduck
Casarca cristata (Kuroda, 1917).—Crested Shelduck
- Subfamily Anatinae** (Leach, 1820).—True ducks; sedis mutabilis ^p
Tribe Malacorhynchini (Boetticher, 1950); incertae sedis ^a
Genus *Malacorhynchus* Swainson, 1831.—Pink-eared ducks
Malacorhynchus membranaceus (Latham, 1801).—Australian Pink-eared Duck

†*Malacorhynchus scarletti* Olson, 1977.—New Zealand Pink-eared Duck

Genus *Salvadorina* Rothschild and Hartert, 1894

Salvadorina waigiensis Rothschild and Hartert, 1894.—Salvadori's Duck

Tribe Anatini (Leach, 1820).—Surface-feeding ducks; incertae sedis ^r

Subtribe Cairinina (Boetticher, 1936–1938).—Long-billed wood ducks

Supergenous *Cairina* Fleming, 1822.—Greater wood ducks

Genus *Cairina* Fleming, 1822.—Muscovy ducks

Cairina moschata (Linnaeus, 1758).—Muscovy Duck

Cairina scutulata (Müller, 1842).—White-winged Duck

Genus *Pteronetta* Salvadori, 1895

Pteronetta hartlaubi (Cassin, 1859).—Hartlaub's Duck

Supergenous *Aix* Boie, 1828

Genus *Aix* Boie, 1828.—Northern wood ducks

Aix sponsa (Linnaeus, 1758).—American Wood Duck

Aix galericulata (Linnaeus, 1758).—Mandarin Duck

Subtribe Nettapodina (Bonaparte, 1856).—Stout-billed wood ducks

Genus *Chenonetta* Brandt, 1836

Chenonetta jubata (Latham, 1801).—Maned Duck

Genus *Nettapus* Brandt, 1836.—Pygmy-geese

Subgenous *Nettapus* Brandt, 1836

Nettapus auritus (Boddaert, 1783).—African Pygmy-geese

Subgenous *Cheniscus* Eyton, 1838.—Pale-rumped pygmy-geese

Nettapus coromandelianus (Gmelin, 1789).—Cotton Pygmy-geese (includes *albipennis* Gould, 1842)

Nettapus pulchellus (Gould, 1842).—Green Pygmy-geese

Subtribe Anatina (Leach, 1820).—Dabbling ducks

Supergenous *Amazonetta* Boetticher, 1929.—Micro-teal

Genus *Amazonetta* Boetticher, 1929

Amazonetta brasiliensis (Gmelin, 1789).—Brazilian Teal (includes *ipecutiri* [Vieillot, 1816])

Genus *Callonetta* Delacour, 1936

Callonetta leucophrys (Vieillot, 1816).—Ringed Teal

Supergenous *Lophonetta* Riley, 1914

Genus *Lophonetta* Riley, 1914

Lophonetta specularioides (King, 1828).—Crested Duck (includes *alticola* Ménégaux, 1909)

Genus *Speculanas* Boetticher, 1929

Speculanas specularis (King, 1828).—Bronze-winged Duck

Supergenous *Anas* Linnaeus, 1758.—True dabbling ducks

Genus indeterminate

†“*Anas*” *theodori* Newton and Gadow, 1893.—Mauritius Duck °

†“*Anas*” *pachyscelus* Wetmore, 1960.—Bermuda Duck °

†“*Anas*” *marecula* Olson and Jouventin, 1996.—Amsterdam Island Duck s

Genus *Mareca* Stephens, 1824.—Wigeons

Subgenus *Notonetta* Roberts, 1922

Mareca capensis (Gmelin, 1789).—Cape Teal

Subgenus *Chaulelasmus* Bonaparte, 1838.—Gadwalls

Mareca strepera (Linnaeus, 1758).—Common Gadwall

Mareca couesi (Streets, 1876).—Washington Island Gadwall †

Subgenus *Eunetta* Bonaparte, 1856

Mareca falcata (Georgi, 1775).—Falcated Duck

Subgenus *Mareca* Stephens, 1824.—Typical wigeons

Mareca sibilatrix (Poeppig, 1829).—Chiloé Wigeon

Mareca penelope (Linnaeus, 1758).—Eurasian Wigeon

Mareca americana (Gmelin, 1789).—American Wigeon

Genus *Anas* Linnaeus, 1758.—Typical dabbling ducks; sedis mutabilis

Subgenus *Anas* Linnaeus, 1758.—Mallards

Infragenus *Melananas* Roberts, 1922

Anas sparsa Eyton, 1838.—African Black Duck (includes *leucostigma* Rüppell, 1845)

Infragenus *Anas* Linnaeus, 1758.—Northern mallards; sedis mutabilis u

Anas rubripes Brewster, 1902.—American Black Duck

Anas platyrhynchos Linnaeus, 1758.—Mallard (includes *conboschas* Brehm, 1831)

Anas fulvigula Ridgway, 1874.—Mottled Duck (includes *maculosa* Sennett, 1889)

Anas diazi Ridgway, 1886.—Mexican Duck

Anas wyvilliana Sclater, 1878.—Hawaiian Duck

Anas laysanensis Rothschild, 1892.—Laysan Duck

Anas oustaleti Salvadori, 1894.—Marianas Duck v

Infragenus *Polionetta* Oates, 1899.—South Pacific mallards

Anas luzonica Fraser, 1839.—Philippine Duck

Anas superciliosa Gmelin, 1789.—Pacific Gray

- Duck (includes *pelewensis* Hartlaub and Finsch, 1872; and *rogersi* Mathews, 1912)
- Anas poecilorhyncha* Forster, 1781.—Indonesian Spot-billed Duck (includes *haringtoni* Oates, 1907)
- Anas zonorhyncha* Swinhoe, 1866.—Chinese Spot-billed Duck
- Infragenus *Afranas* Roberts, 1922.—African mallards
- Anas undulata* Dubois, 1839.—Yellow-billed Duck (includes *rueppelli* Blyth, 1855)
- Anas melleri* Sclater, 1865.—Meller's Duck
- Subgenus *Spatula* Boie, 1822.—Blue-winged ducks
- Infragenus *Pterocyanea* Bonaparte, 1841.—Blue-winged teal
- Anas discors* Linnaeus, 1766.—Blue-winged Teal
- Anas cyanoptera* Vieillot, 1816.—Cinnamon Teal (includes *orinomus* [Oberholser, 1906]; *septentrionalium* Snyder and Lumsden, 1951; *tropica* Snyder and Lumsden, 1951; and *borreroi* Snyder and Lumsden, 1951)
- Infragenus *Spatula* Boie, 1822.—Shovelers
- Anas smithii* Hartert, 1891.—Cape Shoveler
- Anas platalea* Vieillot, 1816.—Red Shoveler
- Anas rhynchotis* Latham, 1802.—Australasian Shoveler (includes *variegata* [Gould, 1856])
- Anas clypeata* Linnaeus, 1758.—Northern Shoveler
- Subgenus *Nesonetta* Gray, 1844.—Australasian teal
- Infragenus *Virago* Newton, 1872.—Gray teal; sedis mutabilis
- Anas bernieri* Hartlaub, 1860.—Madagascan Teal ^w
- Anas gibberifrons* Müller, 1842.—Indonesian Gray Teal
- Anas gracilis* Buller, 1869.—Australasian Gray Teal (includes *remissa* Ripley, 1942) ^x
- Anas albogularis* (Hume, 1873).—Andaman Teal
- Infragenus *Nesonetta* Gray, 1844.—Reddish teal
- Anas castanea* (Eyton, 1838).—Chestnut Teal
- Anas chlorotis* Gray, 1845.—Brown Teal
- Anas aucklandica* Gray, 1844.—Auckland Islands Teal
- Anas nesiotis* (Fleming, 1935).—Campbell Island Teal
- Subgenus *Dafila* Stephens, 1824.—Pintails
- Infragenus *Paecilonitta* Eyton, 1838.—Pale-cheeked pintails
- Anas bahamensis* Linnaeus, 1758.—White-cheeked Pintail (includes *rubrirostris* Vieillot, 1816; and *galapagensis* [Ridgway, 1889])
- Anas erythrorhyncha* Gmelin, 1789.—Red-billed Pintail

- Infragenus *Dafilonettion* Boetticher, 1937.—Speckled teal
Anas flavirostris Vieillot, 1816.—Yellow-billed Teal (includes *oxyptera* Meyen, 1834)
Anas andium (Sclater and Salvin, 1873).—Andean Teal (includes *altipetens* [Conover, 1941])
- Infragenus *Dafila* Stephens, 1824.—Brown pintails
Anas georgica Gmelin, 1789.—Brown Pintail (includes *spinicauda* Vieillot, 1816; and *niceforoi* Wetmore and Borrero, 1946)
Anas acuta Linnaeus, 1758.—Northern Pintail
Anas eatoni (Sharpe, 1875).—Eaton's Pintail (includes *drygalskii* Reichenow, 1904)
- Subgenus *Querquedula* Stephens, 1824.—Holarctic teal
Infragenus *Querquedula* Stephens, 1824
Anas querquedula Linnaeus, 1758.—Garganey Teal
- Infragenus *Nettion* Kaup, 1829.—Green-winged teal
Anas formosa Georgi, 1775.—Baikal Teal
Anas crecca Linnaeus, 1758.—Eurasian Green-winged Teal (includes *nimia* Friedmann, 1948)
Anas carolinensis Gmelin, 1789.—American Green-winged Teal
- Subgenus *Punanetta* Bonaparte, 1856.—Spotted teal
Infragenus *Punanetta* Bonaparte, 1856.—Pale-cheeked teal
Anas versicolor Vieillot, 1816.—Silver Teal (includes *fretensis* King, 1831)
Anas puna Tschudi, 1844.—Puna Teal
- Infragenus *Micronetta* Roberts, 1922
Anas hottentota Eyton, 1838.—Hottentot Teal
- Tribe Aythyini** Delacour and Mayr, 1945.—Pochards
Subtribe Marmaronettina (Livezey, 1996)
Genus *Marmaronetta* Reichenbach, 1853
Marmaronetta angustirostris (Ménétries, 1832).—Marbled Duck
- Subtribe Rhodonessina** (Boetticher, 1950).—Stem pochards
Genus *Netta* Kaup, 1829^y
Subgenus *Netta* Kaup, 1829
Netta rufina (Pallas, 1773).—Red-crested Pochard
Subgenus *Rhodonessa* Reichenbach, 1853
Netta caryophyllacea (Latham, 1790).—Pink-headed Pochard
- Genus *Metopiana* Bonaparte, 1856
Subgenus *Metopiana* Bonaparte, 1856
Metopiana peposaca (Vieillot, 1816).—Rosy-billed Pochard
- Subgenus *Phaeoaythia* Delacour, 1937
Metopiana erythrophthalma (Wied, 1832).—Southern Pochard (includes *brunnea* [Eyton, 1838])

Subtribe Aythyina (Delacour and Mayr, 1945).—True pochardsGenus *Aristonetta* Baird, 1858.—Red-headed pochards*Aristonetta valisineria* (Wilson, 1814).—Canvas-back*Aristonetta americana* (Eyton, 1838).—Redhead*Aristonetta ferina* (Linnaeus, 1758).—Eurasian PochardGenus *Aythya* Boie, 1822.—Typical pochardsSubgenus *Nyroca* Fleming, 1822.—White-eyed pochards^z*Aythya australis* (Eyton, 1838).—Australian White-eyed Pochard (includes *extima* Mayr, 1940)*Aythya innotata* (Salvadori, 1894).—Madagascan White-eyed Pochard*Aythya nyroca* (Güldenstädt, 1770).—Ferruginous White-eyed Pochard*Aythya baeri* (Radde, 1863).—Siberian White-eyed PochardSubgenus *Aythya* Boie, 1822.—Scaup*Aythya novaeseelandiae* (Gmelin, 1789).—New Zealand Scaup*Aythya collaris* (Donovan, 1809).—Ring-necked Scaup*Aythya fuligula* (Linnaeus, 1758).—Tufted Scaup*Aythya marila* (Linnaeus, 1761).—Greater Scaup (includes *mariloides* [Vigors, 1839])*Aythya affinis* (Eyton, 1838).—Lesser Scaup**Tribe Mergini** (Rafinesque, 1815; alternatively, Swainson, 1831).—Seaducks**Subtribe Somaterina** (Reichenbach, 1849–1850).—EidersGenus *Polysticta* Eyton, 1836*Polysticta stelleri* (Pallas, 1769).—Steller's EiderGenus *Somateria* Leach, 1819.—Greater eidersSubgenus *Lampronetta* Brandt, 1847*Somateria fischeri* (Brandt, 1847).—Spectacled EiderSubgenus *Somateria* Leach, 1819*Somateria spectabilis* (Linnaeus, 1758).—King Eider*Somateria mollissima*-group (Linnaeus, 1758).—Common Eider^{aa}*Somateria (m.) v-nigrum* Gray, 1855.—Pacific Eider*Somateria (m.) borealis* (Brehm, 1824).—Northern Eider*Somateria (m.) dresseri* Sharpe, 1871.—Canada Eider (includes *sedentaria* Snyder, 1941)*Somateria (m.) mollissima* (Linnaeus, 1758).—European Eider (includes *islandica* Brehm, 1831; and *faeroeensis* Brehm, 1831)

†Subtribe **Chendytina**, new taxon^{bb}Genus *Chendytes* Miller, 1925*Chendytes lawi* Miller, 1925*Chendytes milleri* Howard, 1955**Subtribe Mergina** (Rafinesque, 1815; alternatively, Swainson, 1831).—Typical seaducksSupergenous *Histrionicus* Lesson, 1828Genus *Histrionicus* Lesson, 1828*Histrionicus histrionicus* (Linnaeus, 1758).—Harlequin DuckSupergenous *Melanitta* Boie, 1822.—Scoters and alliesGenus *Camptorhynchus* Bonaparte, 1838*Camptorhynchus labradorius* (Gmelin, 1789).—Labrador DuckGenus *Melanitta* Boie, 1822.—ScotersSubgenus *Melanitta* Boie, 1822.—White-marked scoters*Melanitta perspicillata* (Linnaeus, 1758).—Surf Scoter*Melanitta fusca* (Linnaeus, 1758).—Velvet Scoter*Melanitta deglandi* (Bonaparte, 1850).—White-winged Scoter (includes *stejnegeri* [Ridgway, 1887])Subgenus *Oidemia* Fleming, 1822.—Black scoters*Melanitta nigra* (Linnaeus, 1758).—Eurasian Black Scoter*Melanitta americana* (Swainson, 1832).—American Black ScoterSupergenous *Mergus* Linnaeus, 1758.—Mergansers and alliesGenus *Clangula* Leach, 1819*Clangula hyemalis* (Linnaeus, 1758).—Long-tailed DuckGenus *Bucephala* Baird, 1858.—GoldeneyesSubgenus *Bucephala* Baird, 1858*Bucephala albeola* (Linnaeus, 1758).—BuffleheadSubgenus *Glaucionetta* Stejneger, 1885*Bucephala clangula* (Linnaeus, 1758).—Common Goldeneye (includes *americana* [Bonaparte, 1838])*Bucephala islandica* (Gmelin, 1789).—Barrow's GoldeneyeGenus *Mergellus* Selby, 1840*Mergellus albellus* (Linnaeus, 1758).—SmewGenus *Lophodytes* Reichenbach, 1853*Lophodytes cucullatus* (Linnaeus, 1758).—Hooded MerganserGenus *Mergus* Linnaeus, 1758.—Typical mergansersSubgenus *Promergus* Mathews and Iredale, 1913^{cc}*Mergus australis* Hombron and Jacquinot, 1841.—Auckland Islands MerganserSubgenus *Prister* Heine, 1890

- Mergus octosetaceus* Vieillot, 1817.—Brazilian Merganser
- Subgenus *Mergus* Linnaeus, 1758.—Greater mergansers
- Mergus merganser* Linnaeus, 1758.—Common Merganser (includes *orientalis* Gould, 1845; and *americanus* Cassin, 1852)
- Mergus serrator* Linnaeus, 1758.—Red-breasted Merganser (includes *schioeleri* Salomonsen, 1949)
- Mergus squamatus* Gould, 1864.—Chinese Merganser
- Tribe Oxyurini** (Phillips, 1926).—Stiff-tailed ducks and allies
- Subtribe Heteronettina** (Boetticher, 1950)
- Genus *Heteronetta* Salvadori, 1865
- Heteronetta atricapilla* (Merrem, 1841).—Black-headed Duck
- Subtribe Oxyurina** (Phillips, 1926).—Stiff-tailed ducks
- Supergenous *Nomonyx* Ridgway, 1880
- Genus *Nomonyx* Ridgway, 1880
- Nomonyx dominicus* (Linnaeus, 1766).—Masked Duck
- Supergenous *Oxyura* Bonaparte, 1828.—Typical stiff-tailed ducks
- Genus *Oxyura* Bonaparte, 1828.—Ruddy (blue-billed) ducks
- Subgenus *Oxyura* Bonaparte, 1828
- Oxyura jamaicensis* (Gmelin, 1789).—Northern Ruddy Duck (includes *rubida* Wilson, 1814)
- Subgenus *Cerconectes* Wagler, 1832; *sedis mutabilis*
- Oxyura ferruginea* (Eyton, 1838).—Peruvian Ruddy Duck^{dd}
- Oxyura vittata* (Philippi, 1860).—Argentine Ruddy Duck
- Oxyura australis* Gould, 1836.—Blue-billed Duck
- Oxyura maccoa* (Eyton, 1836).—Maccoa Duck
- Oxyura leucocephala* (Scopoli, 1769).—White-headed Duck
- Genus *Biziura* Stephens, 1824.—Musk-ducks
- Biziura lobata* (Shaw, 1796).—Australian Musk-Duck
- †*Biziura delautouri* Forbes, 1892.—New Zealand Musk-Duck

^a Adoption by Livezey (1995a) of two of four subgenera of *Dendrocygna* erected by Boetticher (1949) was performed under the Principle of First Reviser (International Commission on Zoological Nomenclature, 1985:Article 24).

^b Several other fossil taxa from the Miocene may be assignable to *Mionetta* (Livezey and Martin, 1988; see also Cheneval, 1987), including: *Anas*[?] *consobrina* Milne-Edwards, 1867; and *Anas*[?] *natator* Milne-Edwards, 1867.

- ^c Partition of complex into orange-billed, taiga-breeding form and largely black-billed, tundra-breeding form is provisional.
- ^d Position tentative, genus may be synonymous with *Branta* (Livezey, 1996a).
- ^e Probably includes several phylogenetic species; one geo-phenotypic partitioning of subspecific taxa is shown (Livezey, 1996a).
- ^f Relationships among some *Cygnus* not resolved (Livezey, 1996a), and Maltese fossil swans provisionally placed based on Northcote (1982, 1988, 1992).
- ^g Provisionally placed based on Livezey (1989a).
- ^h Position of tribe provisional (Livezey, 1996a).
- ⁱ Based on Livezey (1986b) and Livezey and Humphrey (1992).
- ^j Genus may comprise 3–5 sibling species; weak support for segregating the three southern forms from the two northern forms.
- ^k Tribal taxon for this genus in Livezey (1986a), Sarkidiornini, was incorrectly derived and should have been Sarkidiornithini (the same change in stem would apply to corresponding subtribal name); authorship for the family-group name is Oberholser, 1918 (Sarkidiornithinae).
- ^l Provisionally placed based on Livezey (1989a) and subsequent assessments of related genera (Livezey, 1996b).
- ^m Provisionally placed based on codings of characters for limited fossil elements (unpublished data).
- ⁿ Relationships among *C. hybrida*, *C. picta*, and the sister species *C. poliocephala* and *C. rubidiceps* unresolved (Livezey, 1997a).
- ^o Generic assignment based on codings of characters for limited fossil elements (unpublished data) and/or published descriptions.
- ^p Relationships among tribes in Subfamily Anatinae not resolved (Livezey, 1996b).
- ^q Composition of tribe and its inclusion in Subfamily Anatinae provisional (Livezey, 1996b).
- ^r Monophyly of the Tribe Anatini not confirmed (Livezey, 1996b).
- ^s Generic placement within supergenus not possible based on available specimens.
- ^t Recognition of species provisional (Livezey, 1993a).
- ^u Relationships and species status of included taxa unresolved (Livezey, 1991); *A. wyvilliana* and *A. laysanenesis* assignable to *Horizonetta* Oberholser, 1917.
- ^v Possibly of hybrid origin (Yamashina, 1948; Ripley, 1957; Livezey, 1991), and evidently extinct (Reichel and Lemke, 1994).
- ^w Subgeneric assignment tentative (Livezey, 1991).
- ^x Segregation of *A. gracilis* from *A. gibberifrons* at species level follows osteological evidence presented by Ripley (1942), Mees (1982), and Parker et al. (1985).
- ^y Correction of mistaken attribution of seniority to *Rhodonessa* by Livezey (1996c).
- ^z Relationships between the sister species *A. nyroca* and *A. baeri* and other white-eyes remain unresolved (Livezey, 1996c).
- ^{aa} May comprise two or more sibling species (Livezey, 1995c); it is recommended minimally that *v-nigrum* be segregated.
- ^{bb} Position of genus provisional (Livezey, 1993b).
- ^{cc} Provisionally includes sibling species from the Chatham Islands and South Island, New Zealand (Livezey, 1995c).

^{dd} *Oxyura (j.) andina* Lehmann, 1946 (Colombian Ruddy Duck) is provisionally considered here to pertain to hybrid progeny of *O. (j.) jamaicensis* and *O. ferruginea* (Livezey, 1995b).

DISCUSSION

Points of Consensus and Controversy

Graded Classes of Support.—In order to provide an assessment of the relative empirical support of taxonomic groupings defined in the classification, I discuss below selected taxa under five provisional classes based on the evidence presented in the associated analyses (Livezey, 1986a, 1986b, 1986c, 1989a, 1989b, 1990, 1991, 1993a, 1993b, 1995a, 1995b, 1995c, 1996a, 1996b, 1996c, 1997a, 1997b) and a familiarity with the underlying characters. The lists are not intended to be exhaustive, and therefore interpretations of support may not given for some taxa of interest; for such groups, the reader is invited to examine the original analyses.

Practically Unassailable.—Among the higher taxonomic groups for which I consider that monophyly has been established beyond a reasonable doubt are: Order Anseriformes, Suborder Anhimae, Suborder Anseres, Superfamily Anatoidea (including *Presbyornis*), and Family Anatidae. The monophyly of many polytypic genera also has been established using a variety of characters; these genera include *Chauna*, *Cygnus*, *Tachyeres*, *Somateria*, *Mergus*, and *Oxyura* (sensu stricto).

Strongly Supported.—Contrary to the arguments of Feduccia (1980, 1996), Olson and Feduccia (1980), and Olson (1985), the position of the Galliformes as the sister order of the waterfowl is supported by substantial evidence from both morphological and molecular studies (Livezey, 1997b), therefore justifying the Superorder Galloanserimorphae. Monophyly has been well demonstrated for the node uniting the subfamilies Tadorninae and Anatinae, as well as those defining the Tribe Thambetochenini, Subtribe Tadornina, Subtribe Aythyina, Subtribe Oxyurina, and Supergenous *Mergus*. Strong support also is known for several polytypic genera, including *Dendrocygna*, *Somateria*, the subgenus *Olor*, as well as a number of species groups (*Chloephaga poliocephala* and *C. rubidiceps*; *Bucephala clangula* and *B. islandica*).

Moderately Supported.—Adequate but suboptimal support attends a number of inferred groups of Anseriformes. These include the tribes Cygnini, Mergini, and Oxyurini; Subtribe Somaterina; genera *Chloephaga*, *Aristonetta*, *Melanitta*, *Bucephala*, *Oxyura*; Subgenus *Nyroca*; and a number of species groups (*Casarca tadornoides* and *C. variegata*; *Aythya fuligula*, *A. affinis*, and *A. marila*; *Somateria* exclusive of *fischeri*).

Weakly Supported.—Marginally supported nodes and associated taxonomic groups include the subfamilial position of the tribes Thambetochenini (Anserinae or Tadorninae) and Malacorhynchini (Tadorninae or Anatinae), monophyly of the Subfamily Dendrocygninae and the subtribes Chloephagina and Mergina, the node uniting *Mergellus* with its sister genus, monophyly of the genera *Anser* and *Branta*, and monophyly of a number of subgenera and species groups in most anatid tribes (especially within the Dendrocygnini, Anserini, Tadornini, Anatini, Aythyini, and Oxyurini). Also, for reasons detailed elsewhere (Livezey, 1996c), the position of *Aythya collaris* within the Subtribe Aythyina remains problematic. Finally, the positions of many fossil taxa remain tentative, notably those of *Euranas*, *Centronis*, *Anabernicula*, and *Pachyanas*.

Unresolved.—Monophyly of the subfamilies Tadorninae and Anatinae has not

been demonstrated; provisional support for the naturalness of these two groups hinges on ancillary analytical methods, e.g., weighting of osteological characters more heavily than those of plumages (Livezey, 1996b). No single, empirically preferable reconstruction is available for the phylogenetic relationships among members of the following groups: *Olor* group of swans, tribes within the Tadorninae, tribes within the Anatinae, and subtribes within the Anatini. Also unresolved are: the subgeneric placement of *Anas bernieri* (Anatini), relationships within the subgenus *Nyroca* (Aythyini), the sister group of *Oxyura jamaicensis*, and relationships among several members of the *Anas platyrhynchos* group (Anatini). Also, relationships within *Branta canadensis*, *Merganetta armata*, and *Somateria mollissima*, three taxa traditionally considered monospecific but possibly comprising several species, require concerted reassessment.

Future Directions

Much remains to be done concerning the study of the evolution of waterfowl, and these understudied topics include more than confirmatory systematic investigations and attention to areas of poor resolution. In addition to the use of this classification for organizational purposes (e.g., Madge and Burn, 1988) and the refinement of the consensus concerning the phylogeny of Anseriformes (e.g., Christidis and Boles, 1994), it is hoped that the preceding classification will facilitate the use of the underlying phylogenetic hypothesis for comparative study. Appropriate topics for such explorations, some of which have been examined already in a phylogenetic context, include: nest parasitism (Eadie et al., 1988; Rohwer and Freeman, 1989), parental care (Johnsgard and Kear, 1968; Kear, 1970; Scott and Clutton-Brock, 1989), natal vocalizations (Kear, 1968), parameters of reproduction (Rohwer, 1988), morphological convergence (Faith, 1989), brood amalgamation (Beauchamp, 1997), evolutionary patterns in flightlessness and ontogeny (Livezey and Humphrey, 1986; Livezey, 1989b, 1990, 1993a, 1993b, 1995d), historical biogeography (Livezey, 1991, 1996a, 1997a), and diel activity patterns (McNeil et al., 1992).

Courtship behavior, one of the first behavioral aspects of waterfowl to be subjected to intense study (Lorenz, 1941; Delacour and Mayr, 1945; Johnsgard, 1961a, 1965a; Johnsgard and Carbonell, 1996), especially merits reassessment within a phylogenetic context. Indeed, behavioral characters merit consideration as characters in primary phylogenetic reconstruction (de Queiroz and Wimberger, 1993; Wimberger and de Queiroz, 1996), although problems of homology, inadequate data for many species, and variation among studies in the treatment of rare or infrequent behavioral patterns render suspect any analyses based uncritically on the ethological literature (e.g., Irwin, 1996). Myriad other aspects of the evolution of waterfowl await study, and as the availability of quantitative methods for phylogenetic assessments improves (Brooks and McLennan, 1991; Harvey and Pagel, 1991; Martins and Hansen, 1996; Ridley and Grafen, 1996), the revelation of patterns extendable to fossil taxa and other avian groups can be expected in the near future.

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APPENDIX

Characters Used in Preliminary Analyses of Miscellaneous Genera and Species Groups

Branta canadensis Complex

A tentative partitioning of the complex into five geographically integritous, phenotypically congruent forms is adopted, based on three external characters:

1. Body size (mean mass, kg), ordered: (a) small, 1.5–2.0 (other *Branta* spp., *B. [c.] minima*, *B. [c.] hutchinsii*); (b) medium, 2.1–3.9 (all other *B. canadensis*); (c) large, 4.0–5.2 (*B. [c.] moffitti*, *B. [c.] maxima*).
2. Brown color of ventrum: (a) pale (all others); (b) dark (*B. [c.] minima*, *B. [c.] occidentalis*, *B. [c.] fulva*).
3. Narrow white collar at base of neck: (a) typically absent (other *Branta*); (b) typically present (*B. [c.] leucopareia*, including “*asiatica*”). Note: also occurs uncommonly to rarely in *B. (c.) taverneri* and *B. (c.) minima*; possibly treat as intermediate state or polymorphism.

Sarkidiornis Complex

Two allopatric species are recognized based on color of contrasting, uniformly dark sides and flanks.

1. Sides and flanks: (a) gray (*S. melanotos*); (b) black (*S. sylvicola*).

Merganetta Complex

Five diagnosable, parapatric taxa are tentatively recognized. Provisional diagnostic characters (for adult males) include:

1. Black suborbital stripe (adult males): (a) absent (other *Merganetta*); (b) present (*M. armata*).
2. Contrastingly black chin and throat (adult males): (a) absent (other *Merganetta*); (b) present (*M. armata*).
3. Venter, contrastingly black color (adult males, ordered): (a) absent (other

Merganetta [berlepschi variable]); (b) present, confined to breast (*M. armata*); (c) present, including entire ventrum (*M. turneri*).

4. Ground color of venter, rusty color (adult males): (a) absent (*Merganetta colombiana* and *M. leucogenis*); (b) present (other *Merganetta* [very dark in *turneri*, *berlepschi*]).

5. Mantle, at least lateral margins (adult males): (a) black and white striped (others, including *Merganetta armata*, *M. garleppi* [intermediate, variable]); (b) black and brown striped (*M. leucogenis*, *M. colombiana*, *M. turneri*).

6. Mantle, medial portion, black color (adult males): (a) absent (other *Merganetta*); (b) present (*M. turneri*, *M. leucogenis*).

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